Ant communities along an elevational transect, the Udzungwa Mountains in Tanzania

by

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Submitted in fulfilment of the academic requirements of

Master of Science

in Entomology

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg

South Africa

May 2020

PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Biology, School Life Sciences, College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The research was financially supported by National Research Foundation (NRF).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Signed: Supervisor Dr Caswell Munyai

Date: May 2020

Signed: Co-Supervisor Professor Stefan Foord

Date: May 2020

DECLARATION 1: PLAGIARISM

I, Caroline Kunene declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

(vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

Signed: Caroline Kunene

Date: May 2020

DECLARATION 2: CONFERENCE PROCEEDINGS AND DISCLAIMER

Please note that chapter two and chapter three of this thesis were written as standalone papers and therefore some repetition was unavoidable.

Kunene C., Foord S.H. & Munyai T.C. "Ant communities along an elevational transect, Udzungwa Mountain, Tanzania" Biodiversity Information Management Forum (BIMF) and Foundational Biodiversity Information Programme (FBIP) Forum, Eastern Cape, Cape St Francis Resort, 13-16 August 2018. Oral Presentation.

Kunene C., Foord S.H. & Munyai T.C. "Ant communities along an elevational transect, Udzungwa Mountain, Tanzania" Savanna Science Network Meeting, Kruger National Park, Skukuza, 4-8 March 2019. Oral Presentation.

Kunene C., Foord S.H., Malumbres-Orlate & Munyai T.C. "Ant diversity patterns along the Udzungwa mountains: Does it increase or decrease with elevation?" Entomology Society of Southern Africa, Umhlanga Ridge, Durban. 8-11 July 2019. Oral Presentation.

Kunene C., Foord S.H. & Munyai T.C. "What structures ant assemblages along the Udzungwa mountains, species turnover or richness differences?" Biodiversity Information Management Forum (BIMF) and Foundational Biodiversity Information Programme (FBIP) Forum, Roodevalley Faircity Hotel, Pretoria. 20-22 August 2019. Oral Presentation.

Signed: Caroline Kunene

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ABSTRACT

Understanding biodiversity patterns and the processes that structure them along environmental gradients has been a topic of major ecological interest. Although relatively well-known, alpha diversity is still poorly understood. It is therefore crucial to investigate alpha diversity patterns as they reveal how diversified species are within a site and identifies processes underlying the co-occurrence of species at a local scale. The patterns and processes related to beta diversity, however, have lagged even more behind. Beta diversity describes the variation in species composition between sites. It reveals whether species turnover or richness differences cause variation in community composition between sites. Together, alpha and beta diversity may provide baseline information for conservation planning, especially in African Tropics. African tropical rainforests, although very diverse, are some of the most threatened and understudied ecosystems of the world. Similarly, although the primary aim in ecology has been to document biodiversity patterns and the processes that structure them, those of invertebrates have lagged behind. As a result, very little is known about African tropical invertebrate patterns and the mechanisms that drive them. The current study, therefore aims (1) describe ant diversity patterns and community assemblages along the Udzungwa mountains, (2) to describe the extent of compositional differences between sites (beta diversity) and (3) to reveal the assembly mechanisms that drive these differences along an altitudinal gradient, Udzungwa Mountains, Tanzania. A standardized pitfall survey was conducted across five elevational transects, each at a distance of 0.1, 1, 20 and 174 km from the first one. Three target elevations which correspond to the three forest types of this mountain (lowland (300-800 m.a.s.l), sub-montane (800-1400), montane (1400-1500)) were selected. A total of 31 776 ant specimens were collected. They belong to five subfamilies, 34 genera and 101 species. Species richness declined with increasing elevation. Three species assemblages corresponding to the three forest types

were observed across the mountains. The lowland assemblage was very distinct, while the sub-montane and montane assemblages were closely related. Results show that distance (km) and elevational distance (m.a.s.l) influence variation in community composition (beta diversity). Beta diversity increases with geographic and elevational distance, although more noticeable with elevation. The standardised effect sizes (SES) models suggest that species turnover increases with distance and elevation, while richness differences decrease with distance and elevation. Species turnover plays a significant role in structuring ant communities with increasing elevation while neither species turnover nor richness differences play a significant role in structuring ant communities with increasing geographical distance. The overall findings of this study, therefore, suggest that ants of the Udzungwa mountains are niche conservative, beta diversity is affected by distance and elevation and that species replacement structures ant communities with increasing elevation, while biotic interactions structure ant communities with increasing distance. Therefore, temperature is very important in structuring ant communities along the Udzungwa mountains and complementarity between sites is maximized by choosing sites that are at different elevations.

ACKNOWLEDGMENTS

I would like to thank God for giving me the strength and wisdom to see this through. I would also like to thank Him for His endless love and providences, “For of Him, and through Him, and to Him, are all things: to whom be glory for ever. Amen.” – Romans 11:36.

To my supervisor Dr Caswell Munyai, thank you! Thank you for your guidance and support. A lot went into the completion of this thesis and I am grateful to have had a supervisor like you, who cared about both my academic and social wellbeing. Thank you for exposing me to conferences, fieldworks and other activities that have sharpened my research skills, and I hope to carry your infectious work ethic everywhere I go. I am also very grateful to my co-supervisor, for his insightful feedback and assistance with statistical analysis. To Dr Malumbres-Olarte and the University of Copenhagen, Zoological Museum, thank you for trusting us with your samples and your contribution to my data chapters.

To my parents that I love, thank you for supporting me no matter what. Thank you for moulding me into this strong, challenge driven lady that I am, for always encouraging me to try again, to push harder and to work diligently. Nothing makes me happier than just seeing how proud you are of me. I am grateful for my siblings (Mlondi, Zana and Thabiso), thank you for always cheering me on, I love you. Thank you to my friends; Mbali Khumalo, Nonkululeko Ngcobo, Simangenkosi Magagula, Sbongakonke Sosibo, Nduduzo Ntuli for the amazing love and support.

Thank you to the Ant Lab; Nomathamsanqa Mkhize, Sbongiseni Xolo, Nokubonga Thabethe, Snenhlahla Mntambo, Sphesihle Mkhungo, Lindiwe Khoza and Concialia Mukanga for always being there to bounce off ideas, blow off some steam or just to have a good laugh. It is these things that got me through most days.

I am more grateful to the National Research Foundation (NRF) for funding this project.

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CHAPTER 1: INTRODUCTION

For decades, the primary aim in ecology has been to document biodiversity patterns across ecological gradients. Similarly, the primary mechanisms and processes underlying biodiversity patterns along gradients has received considerable attention (Sanders, 2002; Willig et al., 2003; Kaspari et al., 2004; Szewczyk and McCain, 2016). The latter has gained momentum recently as we are entering the Anthropocene and humankind is geared to develop conservation measures due to projected negative impacts of climate change (Bellard et al., 2012), habitat loss (Brooks et al., 2002) and various other anthropogenic activities on biodiversity (Meineke et al., 2018).

Biodiversity is the variability among living organisms in all ecosystems and the ecological complexes involved (Hamilton, 2005). Much of it is concentrated in tropical rainforests (Harrison, 2005) as a result of their lack of seasonal variability in temperature (Janzen, 1967). The lack of seasonal variability creates temperature stratification, narrowing the temperature ranges of tropical species (Hua, 2016). It also lowers species dispersal abilities across elevations as species adapted to certain elevational temperatures cannot move to other elevations (Hua, 2016). It is, therefore, important to understand biodiversity patterns and possibly reveal the factors that allow high concentration of biodiversity along elevations in order to be able to inform conservation programmes.

Tropical rainforests are associated with elevational gradients. These gradients are a powerful model system used to study the effects of environmental changes on biodiversity (Körner, 2007). They are of great interest because they show great variation in environmental conditions within a short geographic distance and are well replicated across space (Rahbek, 1995). Elevational gradients have yielded multiple biodiversity patterns for multiple taxa, for example mammals (McCain, 2007), plants (Manish et al., 2017), amphibians and reptiles (Willig and

Presley, 2016), birds (Rahbek, 1997; McCain, 2009) and also arthropods (Munyai and Foord, 2012; Malumbres-Olarte et al., 2018).

Two general patterns have been observed across elevational gradients; a decline in species richness with increasing elevation (Stevens, 1992; Brühl et al., 1999; Rahbek, 2005; Le Cesne et al., 2015) and mid-elevational peak in species richness (Colwell and Lees, 2000; Sanders, 2002; Munyai and Foord, 2012). Some studies have reported an increase of species richness with increasing elevation (Brehm et al., 2003; Sanders et al., 2003; Malumbres-Olarte et al., 2018) while others observed no clear pattern (Botes et al., 2006). Generally, these patterns have been suggested to be largely driven by the biology of the taxa being investigated, climatic conditions and geometric constraints (Gillette et al., 2015). Several other hypotheses have been proposed to explain these patterns *Viz.* thermal energy hypothesis, mid-domain effect, the effect of area and elevation climatic model (Szewczyk and McCain, 2016).

The thermal energy hypothesis is a temperature-based hypothesis which suggest that there is a close relationship between temperature and species diversity (Kaspari et al., 2004). It predicts that warmer climatic conditions result in longer foraging periods, increased primary productivity and increased metabolic and chemical reactions that lead to faster ecological and evolutionary processes (Allen et al., 2002), therefore, species richness will decrease with decreasing temperature (Allen et al., 2002; Malsch et al., 2008; Szewczyk and McCain, 2016). The mid-domain effect best describes a mid-elevation peak in species richness (McCain, 2009). It is a null model based on spatial domain imposed geometric constraints and predicts that species richness will peak at mid-elevation as a result of geometric constraints affecting the distribution of species ranges (Colwell et al., 2004) and has been documented for various taxa (Rahbek 1997; McCain, 2004, 2007, 2009). The area hypothesis emphasises that increased area results in larger species populations (Gaston, 2000) and more habitats for species to inhibit (Rosenzweig and Abramsky, 1993) which encourage the increase in species richness. However,

because area shrinks with elevation, area hypothesis has been used by Sanders (2002) and Dunn et al. (2010) to explain a decrease in species richness along elevational gradients. The elevation climatic model is dependent on a mountain's local climate. It predicts that the combination of temperature and precipitation are the drivers of diversity. Elevations that are warmer and wetter exhibit the highest diversity (Brown, 2001; McCain, 2007). On arid mountains, diversity is highest at mid-elevations where there is an optimal combination of higher temperatures and higher moisture (Sanders et al., 2003). In wet mountains however, diversity is highest at low elevations, and lowest at high altitudes due to extreme temperature (McCain, 2007). These drivers vary however, with spatial scale. The latter are mainly associated with diversity on a local scale (alpha diversity) and to better understand biodiversity conservation, authorities need to categorise biodiversity into its spatial components as introduced by Whittaker (1960).

Whittaker (1960) first introduced biodiversity as three different components working at different scales. Alpha diversity, beta diversity and gamma diversity. Alpha diversity describes the variability of species at local scales (Whittaker, 1960; Whittaker, 1972). It is often expressed as the number of species (species richness) within a site (Whittaker et al., 2001) and is an important measure of biodiversity because species are a fundamental descriptive unit of analysis in different disciplines including ecology and conservation biology (Sites Jr and Marshall, 2004). Alpha diversity is also important because it reveals processes underlying the co-occurrence of species at a local scale (Swenson et al., 2012). Alpha diversity patterns and the processes associated with these patterns can be used for conservation planning at local scales, however, coupled with beta diversity patterns and the processes shaping them, these two components of diversity could better inform conservation especially at a regional scale (Condit et al., 2002).

Beta diversity is a measure of variation between sites (Whittaker, 1960; Whittaker, 1972; Tuomisto, 2010; Anderson et al., 2011). It reveals what makes species assemblages more or

less similar from each other in a given time and space (Vellend, 2010). Beta diversity provides a link between diversity at local (alpha diversity) and regional (gamma diversity) scales (Whittaker, 1960; Whittaker, 1972) making it a good measure to observe the dynamics of biodiversity patterns (Soininen et al., 2007; Soininen et al., 2018). It can describe how communities respond to several threats of biodiversity, such as anthropogenic activities (Vellend et al., 2007) and climate change (Leprieur et al., 2011) at different environmental gradients (Anderson et al., 2011) by quantifying biodiversity loss (Socolar et al., 2016). Beta diversity has therefore been identified to provide information that best inform conservation strategies (Condit et al., 2002; Qian, 2009; Socolar et al., 2016).

Beta diversity is a multifaceted component of biodiversity (Bishop et al., 2015). It has multiple definitions (Tuomisto, 2010; Anderson et al., 2011) as well as approaches to quantify it (Vellend, 2001; Koleff et al., 2003; Jost et al., 2010). For decades the distance decay in similarity was used to describe how species composition between two communities vary with geographic distances (Soininen et al., 2007) and has been reported (Nekola and White, 1999) to be a result of a decrease in similarity of environmental conditions between sites at different distances, spatial configuration and the nature of landscapes that limits/allows dispersal of species and the neutral theory (Nekola and White, 1999; Hubbell, 2001). More recently, however, the partitioning of beta into its relative components provides a powerful tool for analysing the processes responsible for species composition of different species communities (Baselga, 2010; Carvalho et al., 2012) and if linked with distance decay could illuminate the decreasing similarity between communities with increasing distance, which might be related to the key drivers of beta diversity (Foord and Dippenaar-Schoeman, 2016).

Baselga (2010) proposed a conceptual and methodological framework partitioning beta diversity (B_{total}) into species turnover (B_{sim}) and nestedness-resultant (B_{nes}) components.

However, some authors (Almeida-Neto et al., 2012; Carvalho et al., 2012; Legendre, 2014) argue that B_{nes} is not a true measure of nestedness-resultant dissimilarity between sites but is a special case of an ordered pattern of species richness differences that cannot exactly be calculated. Another conceptual and methodological framework partitioning beta diversity (B_{total}) into species replacement (B_{repl}) and richness differences (B_{rich}) was proposed by Carvalho et al. (2012) and Podani and Schmera (2011). B_{repl} is the replacement of a species by another species in another site (Legendre, 2014) while B_{rich} is the loss or gain of species from one site to another (Urban et al., 2006) and disentangling the roles B_{repl} and B_{rich} is important in understanding biodiversity patterns (Baselga, 2010).

Understanding the processes by which communities are structured and maintained and how these processes vary over temporal, environmental and spatial gradients is important in community ecology (Urban et al., 2016; Ford and Roberts, 2018; Pouteau et al., 2019). It has been widely reported that niche assembly processes, dispersal assembly processes and a neutral theory as proposed by Hubbell (2001) structure community assemblages (Keil et al., 2012) and that their contribution varies in importance among ecosystems (Ford and Roberts, 2018). Niche assembly processes promote or limit the occurrence of a species in the next site as a result of the environment. It is associated with processes like environmental filtering and inter-specific competition (Stegen et al., 2013). Environmental filtering occurs when species fail to persist in a particular environment because they do not have the suitable phenotypes or traits to cope with specific environmental conditions (Keddy, 1992) while competition occurs when a certain species out competes another for the same resources found within a niche/habitat. Dispersal assembly processes structure a community when the ability of a species to disperse to another site and survive detects whether a species will be present/absent in the next site, (Boulangeat et al., 2012). Hubbell (2001), however, suggests that it is both these processes niche assembly processes and dispersal assembly processes that structure communities.

Along altitudinal gradients, the variation in species communities has been observed to decrease with increasing elevation, owing to range sizes, mechanisms of community assembly as well as dispersal (Kraft et al., 2011). However, patterns of species turnover and richness differences are not well known due to lack of studies partitioning beta diversity into these components (Marini et al., 2013; Nascimbene and Spitale, 2017; Qin et al., 2019). Qin et al. (2019) reported that beta diversity was made up by both species turnover and richness differences in their disturbed sites. Species turnover decreased with increasing elevation owing to change in environmental conditions, particularly temperature and richness differences on the other hand increased with elevation due to dispersal limitations. Nascimbene and Spitale (2017) observed species turnover and richness differences contribute differently to the community assembly of bryophytes and lichens and may reflect the response of these species to temperature increase. The contrasting results as reported by Nascimbene and Spitale (2017) show that the partitioning of beta diversity components may yield different results depending on the taxa being investigated as well as the study area.

The current study was conducted across the Udzungwa Mountain ranges which are a biodiversity hotspot recognised for their high level of endemism as well as their outstanding biodiversity and ecosystem services (Rovero et al., 2009). They are listed amongst the 17 most threatened tropical forest ecosystems of the world due to the influence of climate change and land degradation to biodiversity loss (Myers et al., 2000). There is, therefore, a high demand for conservation strategies in this area as its biodiversity is under threat and most of its species remain unquantified. Multiple studies have documented primates (Rovero et al., 2007; Rovero et al., 2009), plants (Lovett et al., 2006; Lovett and Wesser, 2008) and birds (Dinesen et al., 2001; Burgess et al., 2007) of the Udzungwa mountains, however, invertebrate studies are still lagging (Malumbres-Olarte et al., 2018).

Invertebrates have proven to be a powerful tool in monitoring the environmental change (Andersen and Majer, 2004). Moreover, they are a highly successful group with most of its diversity found in terrestrial (Munyai and Foord, 2015) and aquatic ecosystems (McGeoch et al., 2011). Invertebrates are highly abundant, are well known for their provision of ecosystem services (Anderson et al., 2011; McGeoch et al., 2011) and play an important role as bioindicators within ecosystems. However, they are often excluded from conservation programmes (Cardoso et al., 2011). Therefore, in this study ants were used as model organisms to describe their diversity patterns and community assemblages along the Udzungwa mountains (Chapter 2), to describe the extent of compositional differences between sites (beta diversity) and to reveal the assembly mechanisms that drive these differences (Chapter 3). By disentangling the general underlying causes of species turnover and richness differences along the Udzungwa mountains, the current study aims to provide the first step towards informing conservation planning as proposed by Socolar et al (2016). Alpha diversity patterns can be used to infer how best to conserve at a local scale, while beta diversity can be used to infer how best to conserve at a regional scale.

References

Allen, A. P., Brown, J. H., Gillooly, J. F. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297, 1545-1548.

Almeida-Neto, M., Frensel, D. M., Ulrich, W. 2012. Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010). Global Ecology and Biogeography 21, 772-777.

Andersen, A. N., Majer, J. D. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2, 291-298.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14, 19-28.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134-143.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15, 365-377.

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., Parr, C. L. 2015. Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography 42, 1776-1786.

Botes, A., McGeoch, M., Robertson, H., Niekerk, A. v., Davids, H., Chown, S. 2006. Ants, altitude and change in the northern Cape Floristic Region. Journal of Biogeography 33, 71-90.

Boulangeat, I., Gravel, D., Thuiller, W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecology Letters 15, 584-593.

Brehm, G., Süssenbach, D., Fiedler, K. 2003. Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. Ecography 26, 456-466.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16, 909-923.

Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. Global Ecology and Biogeography 10, 101-109.

Brühl, C. A., Mohamed, M., Linsenmair, K. E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology 15, 265-277.

Burgess, N., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldså, J., Howell, K. M., Kilahama, F. B., Loader, S. P., Lovett, J. C., Mbilinyi, B., Menegon, M., 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation 134(2), 209-231.

Carvalho, J. C., Cardoso, P., Gomes, P. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography 21, 760-771.

Colwell, R. K., Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15, 70-76.

Colwell, R. K., Rahbek, C., Gotelli, N. J. 2004. The mid-domain effect and species richness patterns: what have we learned so far? The American Naturalist 163, E1-E23.

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Núnez, P., Aguilar, S., Valencia, R., Villa, G. 2002. Beta-diversity in tropical forest trees. Science 295, 666-669.

Dinesen, L., Lehmberg, T., Rahner, M. C., Fjeldså, J. 2001. Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. Biological Conservation 99, 223-236.

Foord, S. H., Dippenaar-Schoeman, A. S. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. Journal of Biogeography 43, 2354-2365.

Ford, B. M., Roberts, J. D. 2018. Latitudinal gradients of dispersal and niche processes mediating neutral assembly of marine fish communities. Marine Biology 165, 94.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405, 220.

Gillette, P. N., Ennis, K. K., Domínguez Martínez, G., Philpott, S. M. 2015. Changes in Species Richness, Abundance, and Composition of Arboreal Twig-nesting Ants Along an Elevational Gradient in Coffee Landscapes. Biotropica 47, 712-722.

Hamilton, A. J. 2005. Species diversity or biodiversity? Journal of Environmental Management 75, 89-92.

Harrison, R. D. 2005. Figs and the diversity of tropical rainforests. Bioscience 55, 1053-1064.

Hua, X. 2016. The impact of seasonality on niche breadth, distribution range and species richness: a theoretical exploration of Janzen's hypothesis. Proceedings of the Royal Society B: Biological Sciences 283, 20160349.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography (MPB-32). Princeton University Press.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. The American Naturalist 101, 233-249.

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A., Ricotta, C. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions 16, 65-76.

Kaspari, M., Ward, P. S., Yuan, M. 2004. Energy gradients and the geographic distribution of local ant diversity. Oecologia 140, 407-413.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3, 157-164.

Keil, P., Schweiger, O., Kühn, I., Kunin, W. E., Kuussaari, M., Settele, J., Henle, K., Brotons, L., Pe'er, G., Lengyel, S. 2012. Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. Journal of Biogeography 39, 1473-1486.

Koleff, P., Gaston, K. J., Lennon, J. J. 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72, 367-382.

Körner, C. 2007. The use of 'altitude' in ecological research. Trends in Ecology and Evolution 22, 569-574.

Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science 333, 1755-1758.

Le Cesne, M., Wilson, S. W., Soulier-Perkins, A. 2015. Elevational gradient of Hemiptera (Heteroptera, Auchenorrhyncha) on a tropical mountain in Papua New Guinea. PeerJ 3, e978.

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23, 1324-1334.

Leprieur, F., Tedesco, P. A., Hugueny, B., Beauchard, O., Dürr, H. H., Brosse, S., Oberdorff, T. 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology Letters 14, 325-334.

Lovett, J. C., Marshall, A. R., Carr, J. 2006. Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. African Journal of Ecology 44, 478-490.

Lovett, J. C., Wasser, S. K. 2008. Biogeography and ecology of the rain forests of eastern Africa. Cambridge University Press.

Malsch, A. K., Fiala, B., Maschwitz, U., Mohamed, M., Nais, J., Linsenmair, K. E. 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. Asian Myrmecology 2, 33-49.

Malumbres-Olarte, J., Crespo, L., Cardoso, P., Szűts, T., Fannes, W., Pape, T., Scharff, N. 2018. The same but different: equally megadiverse but taxonomically variant spider communities along an elevational gradient. Acta oecologica 88, 19-28.

Manish, K., Pandit, M. K., Telwala, Y., Nautiyal, D. C., Koh, L. P., Tiwari, S. 2017. Elevational plant species richness patterns and their drivers across non-endemics, endemics and growth forms in the Eastern Himalaya. Journal of Plant Research 130, 829-844.

Marini, L., Bertolli, A., Bona, E., Federici, G., Martini, F., Prosser, F., Bommarco, R. 2013. Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. Global Ecology and Biogeography 22, 450-460.

McCain, C. M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. Journal of Biogeography 31, 19-31.

McCain, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecology and Biogeography 16, 1-13.

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography 18, 346-360.

McGeoch, M. A., Sithole, H., Samways, M. J., Simaika, J. P., Pryke, J. S., Picker, M., Uys, C., Armstrong, A. J., Dippenaar-Schoeman, A. S., Engelbrecht, I. A. 2011. Conservation and monitoring of invertebrates in terrestrial protected areas. Koedoe 53, 131-143.

Meineke, E. K., Davies, T. J., Daru, B. H., Davis, C. C. 2018. Biological collections for understanding biodiversity in the Anthropocene. The Royal Society. Philosophical Transactions Royal Society B 374: 20170386.

Munyai, T., Foord, S. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. Journal of Insect Conservation 16, 677-695.

Munyai, T. C., Foord, S. H. 2015. An inventory of epigeal ants of the western Soutpansberg Mountain Range, South Africa. Koedoe 57, 1-12.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853.

Nascimbene, J., Spitale, D. 2017. Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario. Biological Conservation 216, 26-32.

Nekola, J. C., White, P. S. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26, 867-878.

Podani, J., Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. Oikos 120, 1625-1638.

Pouteau, R., Munoz, F., Birnbaum, P. 2019. Disentangling the processes driving tree community assembly in a tropical biodiversity hotspot (New Caledonia). Journal of Biogeography 46, 796-806.

Qian, H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North America. Global Ecology and Biogeography 18, 327-332.

Qin, H., Dong, G., Zhang, F. 2019. Relative roles of the replacement and richness difference components of beta diversity following the ecological restoration of a mountain meadow, north China. Ecological Informatics 52, 159-165.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18, 200-205.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. The American Naturalist 149, 875-902.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8, 224-239.

Rosenzweig, M. L., Abramsky, Z. 1993. How are diversity and productivity related? in: Ricklefs, R. E, Schluter, D. (Eds.), Species diversity in ecological communities. University of Chicago Press, pp. 52-65.

Rovero, F., De Luca, D. W. 2007. Checklist of mammals of the Udzungwa Mountains of Tanzania. Mammalia 71, 47-55.Rovero, F., Marshall, A. R., Jones, T., Perkin, A. 2009.

The primates of the Udzungwa Mountains: diversity, ecology and conservation. Journal of Anthropological Sciences 87, 93-126.

Sanders, N. J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography 25, 25-32.

Sanders, N. J., Moss, J., Wagner, D. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12, 93-102.

Sites Jr, J. W., Marshall, J. C. 2004. Operational criteria for delimiting species. Annual Review of Ecology, Evolution, and Sytematics 35,199-227.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., Edwards, D. P. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31, 67-80.

Soininen, J., Heino, J., Wang, J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Global Ecology and Biogeography 27, 96-109.

Soininen, J., McDonald, R., Hillebrand, H. 2007. The distance decay of similarity in ecological communities. Ecography 30, 3-12.

Stegen, J. C., Lin, X., Fredrickson, J. K., Chen, X., Kennedy, D. W., Murray, C. J., Rockhold, M. L., Konopka, A. 2013. Quantifying community assembly processes and identifying features that impose them. The International Society for Microbial Ecology Journal 7, 2069-2079.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. The American Naturalist 140, 893-911.

Swenson, N. G., Erickson, D. L., Mi, X., Bourg, N. A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J. K., Liu, X., Ma, K. 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. Ecology 93, S112-S125.

Szewczyk, T., McCain, C. M. 2016. A systematic review of global drivers of ant elevational diversity. PloSOne 11, e0155404.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33, 2-22.

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J., Crozier, L., De Meester, L., Godsoe, W. 2016. Improving the forecast for biodiversity under climate change. Science 353, aad8466.

Urban, M. C., Skelly, D. K., Burchsted, D., Price, W., Lowry, S. 2006. Stream communities across a rural–urban landscape gradient. Diversity and Distributions 12, 337-350.

Vellend, M. 2001. Do commonly used indices of β-diversity measure species turnover? Journal of Vegetation Science 12, 545-552.

Vellend, M. 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology 85, 183-206.

Vellend, M., Verheyen, K., Flinn, K. M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B. J., Bellemare, J., Honnay, O. 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. Journal of Ecology 95, 565-573.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30, 279-338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21, 213-251.

Whittaker, R. J., Willis, K. J., Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28, 453-470.

Willig, M. R., Kaufman, D. M., Stevens, R. D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34, 273-309.

Willig, M. R., Presley, S. J. 2016. Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. Journal of Tropical Ecology 32, 421-436.

CHAPTER 2: Ant diversity declines with increasing elevation along the Udzungwa mountains, Tanzania

Abstract

Tropical rainforests are the most diverse, but maybe the least understood terrestrial ecosystems of the world. The elevational patterns associated with them are understudied, especially for invertebrates. There is, however, evidence of biodiversity following two general patterns a monotonic decline in species richness with increasing elevation or a mid-elevational peak, depending on the taxa and geographic region being investigated. This study, therefore, aims to investigate ant diversity patterns along an altitudinal gradient in the Udzungwa Mountains, Tanzania. It was hypothesized that (1) ant diversity will be concentrated in the lowland forest and will decrease with increasing elevation and (2) each forest type will have a distinct ant assemblage. A standardized survey using pitfall sampling was conducted across five elevational transects, each at a distance of 0.1, 1, 20 and 174 km from the first one. They were at three target elevations which corresponded to three forest types (lowland, 300-800 m a.s.l; sub-montane, 800-1400 m a.s.l; montane, 1400-1500 m a.s.l). Ant species richness declined with increasing elevation perhaps owing to their limited tolerance to the cold at higher elevation. Three ant assemblages associated with the three forest types were observed along the mountain ranges, suggesting that ants are niche conservative. The ant assemblage associated with the lowland forest was very distinct, while assemblages associated with the sub-montane and montane forests shared species. Our findings show that most ant species are found in the lowland forest and that their assemblages are distinct. It seems like this study could be used for conservation and monitoring, regardless of the diversity patterns observed.

Keywords: Ant assemblages, elevational gradients, biodiversity, ants (Hymenoptera; Formicidae), Easter Arc Mountains

2.1 Introduction

One of the central goals in ecology is to understand the distributional patterns of biodiversity and the factors that are responsible for such patterns. The latter allows for the assessment and monitoring of changes in ecosystems as well as biodiversity and assists the development of conservation priorities and policies (Dickinson et al., 1992; Jost et al., 2010; Hoffmann et al., 2018). To be able to reach this goal, we must first quantify and characterize communities across various ecosystems. This involves studying species composition and community structure as well as understanding their variation within a given time and space (Malumbres-Olarte et al., 2018).

Environmental gradients have been widely studied to reveal the distribution of biodiversity across different regions and climatic conditions (McCoy, 1990; Rahbek, 1995; Brown, 2001; Arnan et al., 2014). They are useful because they elucidate the effects of natural changes in the environment on biodiversity. It has been observed that biodiversity changes along environmental gradients, and that the patterns of change are strongly variable (Sanders et al., 2003; Willig et al., 2003; Kaspari et al., 2004). The most documented pattern of biodiversity is the latitudinal gradient of increasing richness from polar regions to the equator (Willig et al., 2003). It has been documented for a wide range of taxonomic groups and reported across different environments (Tittensor and Worm, 2016). Another major environmental gradient that has been studied is the altitudinal gradient. However, patterns along the altitudinal gradients have varied between taxa as well as regions (Munyai and Foord, 2012; 2015; Peters et al. 2016).

Altitudinal gradients are a powerful model systems (Körner, 2007). They provide natural experiments when investigating the distribution of biodiversity as they have a wide range of environmental conditions within small geographic space (Körner, 2007; Bishop et al., 2014).

This makes it particularly easier to test patterns and processes that would occur on a larger scale (Sanders et al., 2007). The prediction that a 100 m rise in elevation lowers air temperature by 0.6 – 1.0℃, limiting species from moving further up the mountain (especially with thermophilic species) suggests that ecosystems at high altitudes (with the predicted 2℃ increase in air temperature by 2100) are more vulnerable to climate change, making studying patterns along altitudinal gradients very important for conservation (Körner, 2007; Wang et al., 2017).

The Udzungwa Mountains are part of the Eastern Arc Mountains, which is a massif stretching from Kenya to Tanzania along the east coast of Africa (Lovett et al., 2006; Rovero et al., 2009). This massif is recognised as a biodiversity hotspot (Myers et al., 2000) and a conservation site for iconic endemic species, such as the Udzungwa red colobus and the Sanjei mangabey (Dinesen et al., 2001; Rovero et al., 2006). It also has the second richest bird biodiversity in Africa (Rovero et al., 2009). Much of its known biodiversity is from avifauna studies (Dinesen et al., 2001; Cordeiro et al., 2006; Romdal and Rahbek, 2009) as well as mammal studies (Marshall et al., 2005; Stanley and Hutterer, 2007; Marshall et al., 2008; Rovero et al., 2009) and very little is known about the local invertebrates.

Ants are a diverse and important group of insects in tropical rainforests (Brühl et al., 1999). They contribute 10-20% of animal biomass in terrestrial ecosystems and are of great ecological importance (Holldobler and Wilson, 1990; Brühl et al., 1999). They are found in all forest strata and serve as herbivores, scavengers and predators. They are ecosystem engineers (Folgarait, 1998) and can be used as biological indicators (Andersen and Majer, 2004). The composition of ants varies along environmental gradients (Wiescher et al., 2012) and their traits that correlate with environmental conditions, therefore making the presence or absence of a particular species a potentially appropriate indicator of environmental stress

(Kaspari and Weiser, 2000; Wiescher et al., 2012). Although ants have been the focus of many elevational studies, a lot more is yet to be revealed about the African tropical ants. Therefore, our findings will contribute to the knowledge of tropical ant patterns and consequently the conservation of these diverse tropics, particularly African tropical forests.

The current study aims to characterise ant communities along an altitudinal gradient in the Udzungwa Mountains and test the following hypotheses: (1) ant diversity will decline with increasing elevation considering that they are largely thermophilic and that (2) they will be distinct ant assemablage composition which correspond to the three forest types along the Udzungwa mountains.

2.2 Methods and Materials

Study Sites Description

The Udzungwa Mountains (7.82° S, 36.70° E) are widely recognized for their outstanding biodiversity and high endemicity (Rovero and De Luca, 2007). They form the largest block of the Eastern Arc Mountains (Burgess *et al*., 2007) covering 10 000 km^2. Their long-term climatic stability has made the mountains to endure through millions of years (Lovett and Wasser, 2008). The altitude ranges from 200 to 2500 m a.s.l. and has heterogeneous habitats which range from the lowland rainforest (300–800 m a.s.l.) covered by deciduous miombo (*Brachystegia* spp); submontane rainforest (700–1400 m a.s.l.) covered by a moist forest consisting of evergreen species; montane rainforest (1400–1800 m a.s.l.) and mountain bamboo forest (2400 m a.s.l.) covered by a mosaic of bamboo (*Sinarundinaria alpina*) and *Hagenia abyssinica* species as described by Shangali et al., (1998). The climate in the Udzungwa Mountains is variable and it receives rainfall between 2000-3000 mm per year, due to the influence of the Indian Ocean (Rovero et al., 2009; Rovero et al., 2017). It has a

heavy rainy season between March and May, and a light rainy season between November and February (Lovett and Thomas, 1986). Our study was conducted in the Udzungwa Mountain National Park, proclaimed in 1992, protecting one fifth of the mountain (Rovero et al., 2009).

Ant sampling

Five elevational transects were set up, each with a 50 m x 50 m square plot at each of the three target elevations (300-800, 800-1400 and 1400-1500 m a.s.l.) which correspond to three different forest types (lowland forest, submontane forest and montane forest, respectively, (Table 2.1)) (Lovett, 1999). The five transects were separated horizontally by 0.1, 1, 20 and 175 km from the first transects (Appendix A).

At each 50m x 50m plot, twelve pitfall samples 4m apart (12 x 4 = 48) were collected on each side of the plot (Appendix A), as part of the application of the Conservation Oriented Biodiversity Rapid Assessment for Tropical Forests (COBRA-TF) sampling protocol (Malumbres-Olarte et al., 2017). They were partly filled with preservative solution (propylene glycol) and a few drops of liquid soap to break surface tension and sheltered using lids on stilts about 2-3 cm above the ground. The traps ran for two weeks.

Samples were washed in the laboratory and stored in 96% ethanol. Ants were identified to genus level using Fisher and Bolton (2016) and then identified to species level where possible using online databases; *viz.* AntWiki (http://www.antwiki.org/) and AntWeb (http://antweb.org/). Number codes were assigned to unidentified ant species and were only identified to genus level and then assigned to morphospecies. Voucher species are held in the Zoological Museum of the Natural History Museum of Denmark, Copenhagen, Denmark.

Table 2. 1: Description of the three studied forest habitat types in the Udzungwa Mountains, Tanzania, modified from (Rovero et al., 2009).

Habitat types	Altitudinal range	Description
Lowland forest (low elevation)	300 – 800	Forest with deciduous and semi-deciduous trees, canopy 15–25 m with emergents to 50 m
Sub montane forest (mid elevation)	800 – 1400	Moist forest with mainly evergreen species, canopy 25–40 m with emergents to 50 m
Montane forest (high elevation)	1400 – 2600	Evergreen moist forest, with canopy height progressively lower with altitude

Data analysis

Sample coverage for species diversity was analyzed in iNEXT online software (Chao et al., 2016). Extrapolation show that a few more species could have been found in the lowland forest, otherwise almost all species were sampled in the sub-montane and montane forest (Appendix B). Sampling completeness based on Chao1 and Jack2 richness estimators was determined using EstimateS (Version 9.1.0) (Colwell, 2013) and graphs were drawn using the R language (R Development Core Team, 2017). The species composition of the ant communities was explored and compared through non-metric multidimensional scaling (nMDS). We used a distance matrix calculated based on Bray-Curtis distance, rank dissimilarity and two dimensions. The comparison of species composition within the three habitat types was conducted using PERMANOVA in R (R Development Core Team, 2017). Characteristic species of each habitat were determined using the Indicator Value Method (IndVal) which uses the degrees of specificity (uniqueness to a particular site) and fidelity (frequency within the vegetation type/aspect) of each species (Dufrêne and Legendre, 1997). An indicator value above 70% shows that a species is both highly specific and has a high fidelity to a given site. The significance of the IndVal values is then tested by random reallocation of replicates among groups (Botes et al., 2006).

2.3 Results

A total of 31 776 ant specimens belonging to five subfamilies, 34 genera and 101 species were collected. Myrmicinae was the most diverse subfamily with 54% of the total abundance, 50% (51 species) of the total number of species and 41% of the total number of genera (Table 2.2). The second most diverse subfamily was Ponerinae with 24% of species and 29% of the total number of genera, followed by Formicinae with 19% of the total species and 18% of the total number of genera. The least diverse subfamilies were Dolichoderinae and Dorylinae with 3% and 4% of the total species richness respectively. However, Dorylinae was the second most abundant subfamily with 42% of all specimens. The most speciose genera were *Tetramorium* (19 species), *Pheidole* (8 species), *Strumigenys* (6 species) while *Camponotus* and *Crematogaster* had five species each.

Table 2. 2: Species richness and abundance of ant subfamilies collected in the study.

Subfamily	Genera	Species	Species Richness (%)	Abundance	Abundance (%)
Dolichoderinae	1	3	2.9	5	0.01
Dorylinae	3	4	3.9	13266	42
Formicinae	6	19	18.8	466	1
Myrmicinae	14	51	50.5	17157	54
Ponerinae	10	24	23.8	882	3

Sampling completeness

According to sampling coverage, sampling was complete for the three habitat types: lowland, sub-montane and montane forest as sampling coverage was close to 1 (Table 2.3). However, extrapolation show that more species in the lowland forest would have been recorded with further sampling (Appendix B).

Table 2. 3: Observed number of species and sample coverage for each sampling plot in the three habitat types (lowland, sub-montane and montane forest).

Habitat type	Plot	Altitude m a.s.l	Observed species richness	Sample coverage
Lowland	1	650	29	0.9963
	2	650	38	0.9967
	7	708	40	0.9939
	13	674	22	0.9893
	16	659	24	0.9748
Sub-montane	3	1005	24	0.9986
	4	993	21	0.9956
	8	978	25	0.9982
	14	1006	15	0.9961
	17	908	13	0.9118
Montane	5	1448	23	0.994
	6	1482	18	1
	9	1527	15	0.9954
	15	1552	15	0.9862
	18	1531	5	0.9863

Species diversity patterns

Ant activity was the highest at mid-elevation and *Myrmicaria rustica angustior* contributed much to it (27% of the total abundance) (Figure 2.1). Ant activity which is the total number of individuals in a plot, was lowest at low elevation (Figure 2.1) even though it was dominated by *Dorylus helvolus*, which also contributed with 27% of the total abundance. Simpsons index of diversity showed that the low elevation was the most diverse (0.664) followed by the mid-elevation (0.4817), with the high elevation being the least diverse (0.4435). Species richness was significantly higher at low elevations (31 ± 8), it decreased at mid-elevations (20 ± 9) and it was the lowest at high elevations (15 ± 7) (Figure 2.2).

Ant assemblage composition across the gradient

The NMDS showed a separation of communities according to their elevations. PERMANOVA confirmed significant differences in species composition between plots at the three elevations (df=2, Pseudo-F= 2.7863, P=0.002). Species composition for the low, mid and high elevations is distinct (Figure 2.3).

Indicator species

Seventy-four percent of the species were found in the lowland forest, while 44% and 33% were collected in the sub-montane and montane forests, respectively. Fifteen species had a wide distribution and occurred in all elevations, 37 species were restricted to the lowland forest, 11 were restricted to the sub-montane and 9 species were restricted to the montane forest (Appendix C, F). However, the latter species were not indicators of the different forest types. Five species were indicators of the lowland forest, two were indicators of the sub-montane forest and two were characteristic of the montane forest (Table 2.4).

Table 2. 4: Indicator values (IndVal) of ant species for forest habitat types along the transects. All indicator values are significant ($p < 0.05$).

Habitat type	Species	Indicator value (%)
Lowland	*Pheidole* sp.05	100
	Megaponera analis rapax	99.52
	Camponotus sp.02. (*etiolipes* gp.)	94.12
	Tetramorium cf. yarthiellum	80
	Nylanderia sp.01	70.77
Sub-montane	*Bothroponera* sp.01	85.71

	Myrmicaria rustica angustior	81.23
Montane	*Tetramorium* sp.14	100
	Mesoponera sp.02	82.61

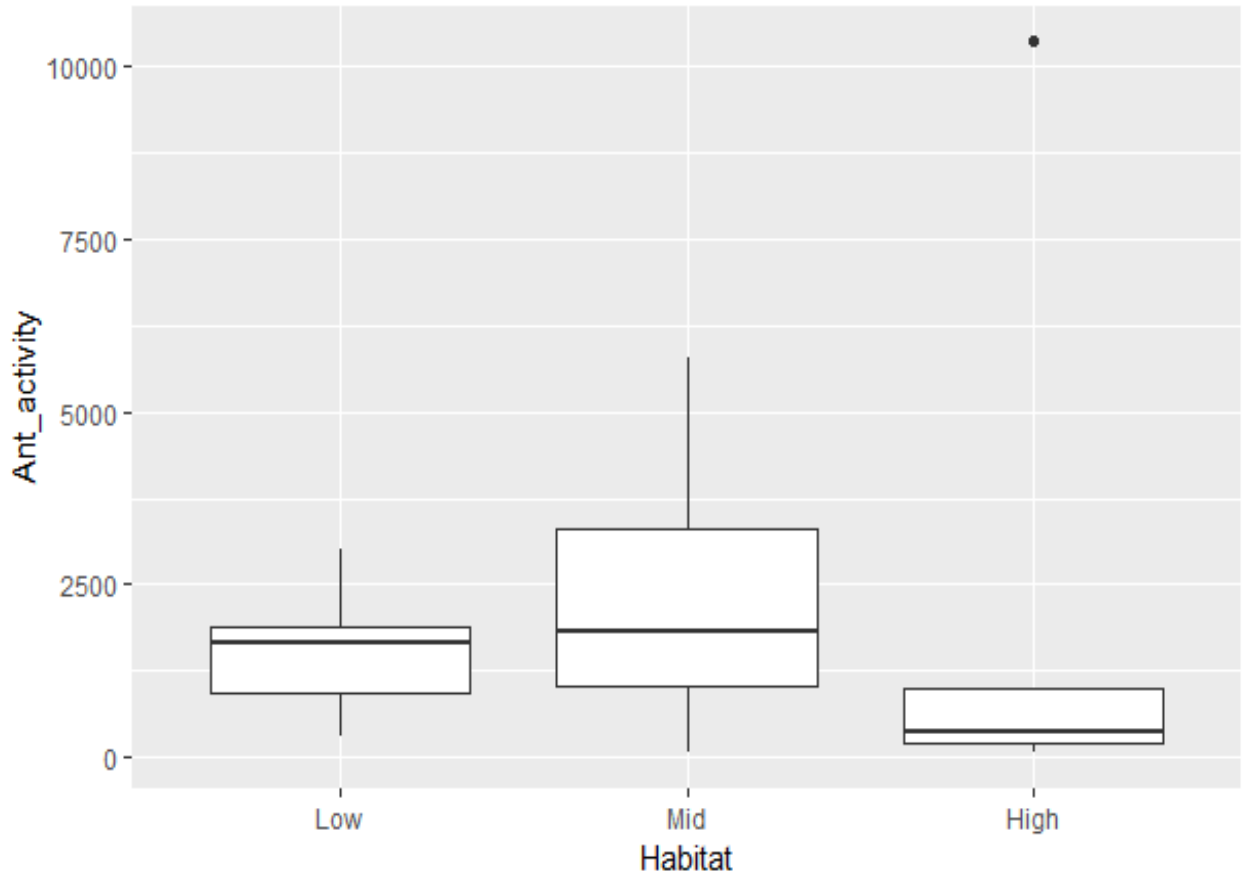


Figure 2. 1: Ant activity across the elevational gradient (low (300-800 m), mid (800-1400 m), high (1400-1500 m).

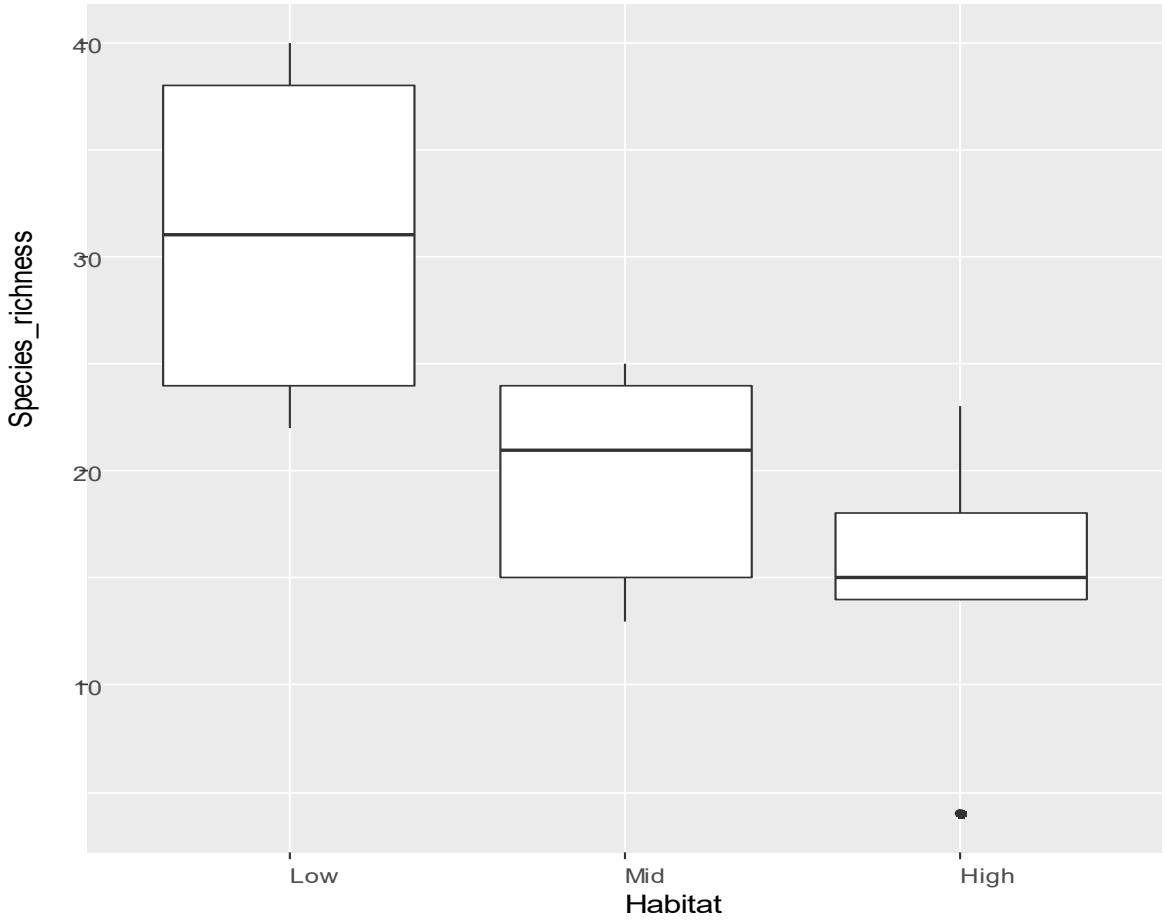


Figure 2. 2: Ant species richness across the elevational gradient (low (300-800), mid (800-1400), high (1400-1500)).

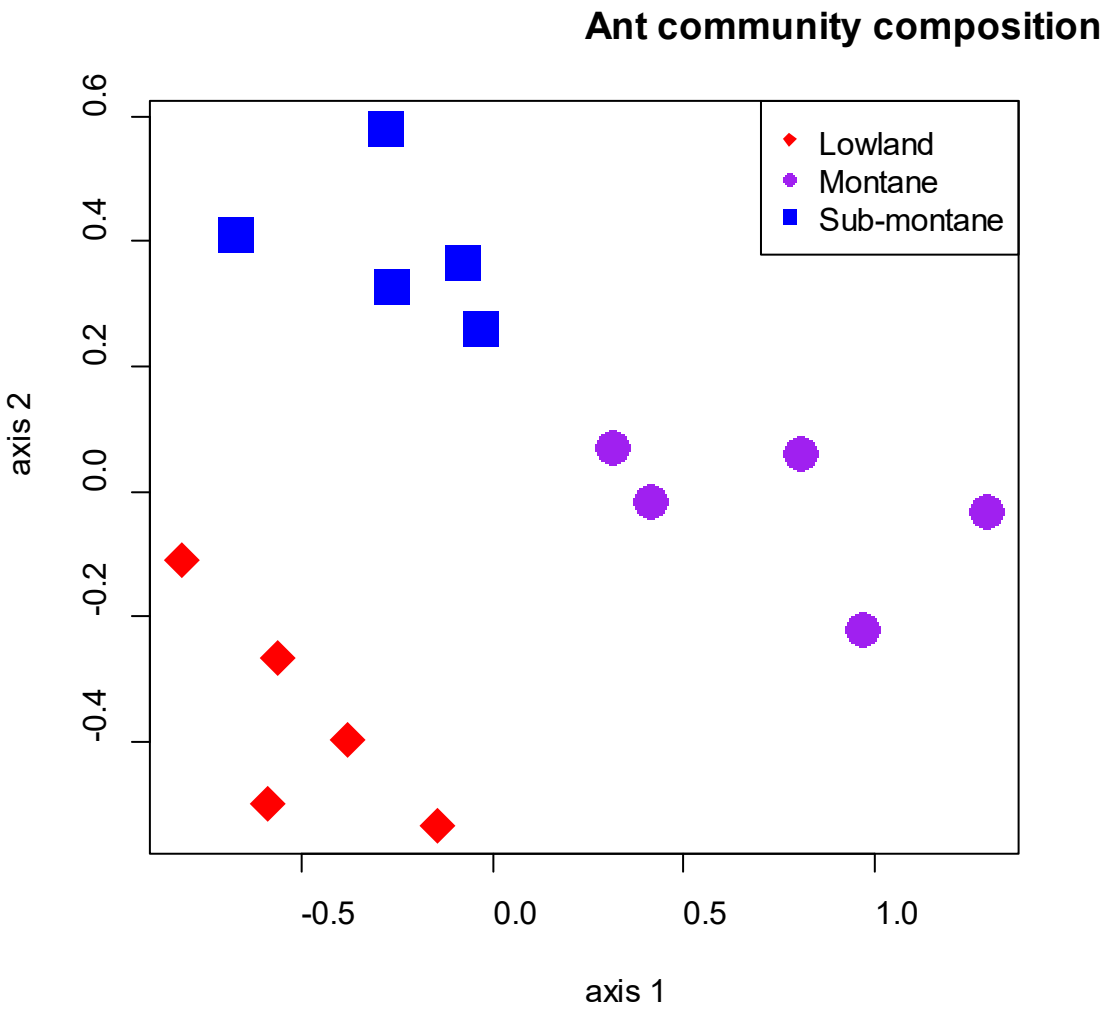


Figure 2. 3: Non-metric multidimensional scaling (NDMS) plot of community similarity (Bray–Curtis dissimilarity index) based on ant species found in three forests types – lowland (red), sub-montane (purple), montane (blue) in the Udzungwa Mountains, Tanzania.

2.4 Discussion

Ant species declined with increasing elevation along the Udzungwa mountains. This is a widely observed pattern along elevational gradients (Stevens, 1992; Grytnes and Vetaas, 2002) but not so much for the other taxa studied across the Udzungwa mountains. Along these mountains, ground dwelling spiders increase with elevation (Malumbres-Olarte et al., 2018), bird richness peaked at mid-elevations (Romdal and Rahbek, 2009) and plants and rodents

increase with elevation (Lovett et al., 2006; Stanley and Hutterer, 2007), opposing patterns of ant richness as reported in the current study.

It is widely accepted that ants are generally a thermophilic group (Kaspari and Weiser, 2000). The distribution of ants is mainly determined by their tolerance to the heat (Dunn et al., 2010), and therefore, a decrease in ant species along an altitudinal gradients may be explained by the decrease in temperature towards the high elevations (Sanders et al., 2007; Bishop et al., 2014). Cooler temperatures may slow down metabolic processes of ants, affect the development of eggs and larvae, affect their foraging activities and consequently their primary productivity (Rosenzweig and Abramsky, 1993).

The limited tolerance of ants to the cold may also cause niche conservatism. This is the tendency of species to retain aspects of their fundamental niche over time (Wiens and Graham, 2005). Mountainous areas are known to have novel set of environmental conditions which act as a barrier, limiting the dispersal of species from one elevation to the next. The latter therefore, creates a difference in species richness between elevations (Wiens and Graham, 2005; Wiens et al., 2010).

In the tropics, lowland species are reported to have very narrow fundamental niches which limits their distribution to the lowland (McCain, 2009), and we found that a great number of ant species were restricted to the lowland forest (Appendix B). These species vary from a rarely encountered cryptic species (*Asphinctopone pilosa*) (Hawkes, 2010), a widely distributed *Technomormyx pallipes* in Afrotropical and Malagasy species, to a common rainforests and evergreen predatory forests species (*Odontomachus assiniensis*), as well as common generalists ant species (*Monomorium mirandum*) (Hawkes, 2010; Garcia et al., 2013). The species restricted to the lowland seem to have specialised to the lowland and they have kept their specialisation over time. As a consequence, they cannot disperse to or survive

in the sub-montane and montane forest. The latter is also supported by the high number of indicator species associated with the lowland forest, emphasizing that more species are specialised to this forest type.

Fewer ant species were restricted to the montane forest (Appendix B) and only two were indicators of this forest type. Some species seemed to have larger distributional ranges as they were found in all three elevational zones. This is typical of tropical species at higher elevations as they tend to be generalists with wider tolerances (Oyen et al., 2016) compared to those in the lowland forests, however, in the current study, species showing wide tolerances were found across the mountain (Appendix B). Amongst them were both generalists and specialised genera such as *Myrmicaria* (tropical climate specialists)*, Pheidole* (generalized Myrmicinae) and *Solenopsis* (hot climatic specialists) (Andersen, 1997). However, all these species may be generalists on these mountains as they have wide geographic distribution and show no habitat preferences.

The two most influential species were *Myrmicaria rustica angustior* and *Dorylus helvolus*. *Myrmicaria rustica angustior* is found in open areas of Afrotropical regions and feeds on other insects (AntWeb, 2019). It contradicts with its habitat preference in this study as it was found throughout the mountain. Its abundance peaked at mid-elevations (Appendix D) perhaps owing to overlapping ranges of the lowland and montane forests resulting in the edges providing more open habitats for ants to inhabit (McCain, 2009). However, *Dorylus helvolus* declined with increasing elevation (Appendix D). Species in genus *Dorylus* are generalist predators that consume any kind of prey ranging from immatures of other insects to vertebrate carrion and this observation might explain their occurrence throughout the mountain (Gotwald Jr, 1995). Moreover, *Dorylus* species are known to move nests in response to prey availability (Schöning and Moffett, 2007) and are most likely to have been

influenced by foraging behaviour, as their colonies migrate to new colonies in irregular intervals resulting in new colonies forming through colony fission (Gotwald, 1995).

Three ant assemblages associated with the three forest types seem to have developed over time. These findings are similar to that of spiders along these mountains (Malumbres-Olarte et al., 2018), however ant assemblages seem to be more distinct. The low elevations (lowland forest) had the most distinct assemblages while high and mid-elevations shared species. Tropical species have narrow elevational ranges as they are adapted to or are exposed to stable local environmental conditions causing them to specialize to those specific conditions (Janzen, 1967). The latter may explain the separation of assemblages with respect to their elevational zones. The distinct low elevation assemblages may be a result of many tropical lowland species having narrow fundamental niches limiting their distribution to the lowland, while other species may occur in more than one elevation as a result of their wider tolerances (Hua, 2016). The homogeneous habitat structure in the Udzungwa Mountains might be the reason for the similarities between the mid and high elevation communities (matching the ideas of spider communities on the same mountain) (Malumbres-Olarte et al., 2018). However, other important factors that structure insect assemblages for example are how specialized species are to resources as well as their physiological tolerances to the climate they are exposed to, might have contributed to this pattern (Stork and Grimbacher, 2006).

In conclusion, our study supports a dominant pattern in tropical mountains; that ant species richness declines with an increase in elevation. It also adds to our knowledge of the distribution of the poorly understood group of animals on this mountain. Secondly three distinct ant assemblages were observed corresponding to the three target elevations/forest types with the lowland forest (low elevation) showing a high variation of species when compared to the montane and sub-montane forest. Conservation along these mountains should

monitor the dynamics of identified indicator species associated with each forest types in order to be able to measure the response of biodiversity to climate change and anthropogenic activities on these mountains.

The importance of prioritizing specific blocks on the Eastern Arc massif like the Udzungwa mountains for conservation has been largely emphasized (Dinesen et al., 2001), however, only biological data of birds, mammals, plants and a few invertebrates indicating "potential trends in importance" have been used to inform this decision. Extensive research including the environmental and climatic factors which might be responsible or the drivers of the reported biodiversity patterns, still needs to be done on the invertebrates of this mountain to better inform conservation strategies. The current study along with Malumbres-Olarte et al. (2018) shows contrasting biodiversity patterns between ants and spiders suggesting that a lot is yet to be revealed and inferred from the invertebrates of the Udzungwa mountains and potentially other areas that have not been prioritized.

References

Andersen, A. N. 1997. Ants as indicators of ecosystem restoration following mining: a functional group approach, in: Hale, P., Lamb, D. (Eds), Conservation Outside Nature Reserves. Brisbane: Centre for Conservation Biology, University of Queensland, pp. 319-325.

Andersen, A. N., Majer, J. D. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2, 291-298.

AntWeb. Available from:

https://www.antweb.org/description.do?genus=myrmicaria&species=rustica&subspecies=angustior&rank=subspecies. Accessed 25 January 2019

Arnan, X., Cerdá, X., Retana, J. 2014. Ant functional responses along environmental gradients. Journal of Animal Ecology 83, 1398-1408.

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., Parr, C. L. 2014. Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. Journal of Biogeography 41, 2256-2268.

Botes, A., McGeoch, M., Robertson, H., Niekerk, A. v., Davids, H., Chown, S. 2006. Ants, altitude and change in the northern Cape Floristic Region. Journal of Biogeography 33, 71-90.

Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. Global Ecology and Biogeography 10, 101-109.

Brühl, C. A., Mohamed, M., Linsenmair, K. E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology 15, 265-277.

Burgess, N., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldså, J., Howell, K. M., Kilahama, F. B., Loader, S. P., Lovett, J. C., Mbilinyi, B., Menegon, M., 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation 134(2), 209-231.

Byrne, L. B. 2007. Habitat structure: a fundamental concept and framework for urban soil ecology. Urban Ecosystems 10, 255-274.

Chao, A., Ma, K., Hsieh, T. 2016. User's Guide for iNEXT Online: Software for Interpolation and Extrapolation of Species Diversity.

Colwell, R. 2013. EstimateS 9.1. 0 user's guide. Connecticut: University of Connecticut.

Colwell, R. K., Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15, 70-76.

Cordeiro, N., Lovett, J., Mulungu, E., Maina, G., Gerstle, J. 2006. Initial trends of bird assemblages before and after river diversion in an endemic-rich African forest. Biodiversity and Conservation 15, 971-983.

Dickinson, K., Mark, A., Lee, W. 1992. Long-term monitoring of non-forest communities for biological conservation. New Zealand Journal of Botany 30, 163-179.

Dinesen, L., Lehmberg, T., Rahner, M. C., Fjeldså, J. 2001. Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. Biological Conservation 99, 223-236.

Dufrêne, M., Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345-366.

Fisher, B. L., Bolton, B. 2016. Ants of Africa and Madagascar: a guide to the genera. University of California Press.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7, 1221-1244.

Garcia, F. H., Wiesel, E., Fischer, G. 2013. The ants of Kenya (Hymenoptera: Formicidae)—faunal overview, first species checklist, bibliography, accounts for all genera, and discussion on taxonomy and zoogeography. Journal of East African Natural History 101, 127-222.

Gibb, H., Parr, C. 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents. Oecologia 164, 1061-1073.

Gotwald Jr, W. H. 1995. Army ants: the biology of social predation. Cornell University Press.

Grytnes, J. A., Vetaas, O. R. 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. The American Naturalist 159, 294-304.

Hawkes, P. G. 2010. A new species of Asphinctopone (Hymenoptera: Formicidae: Ponerinae) from Tanzania. Zootaxa 2480, 27-36.

Hoffmann, S., Schmitt, T. M., Chiarucci, A., Irl, S. D., Rocchini, D., Vetaas, O. R., Tanase, M. A., Mermoz, S., Bouvet, A., Beierkuhnlein, C. 2018. Remote sensing of β-diversity: Evidence from plant communities in a semi-natural system. Applied Vegetation Science 22, 13-26.

Hölldobler, B., Wilson, E. O. 1990. The ants. Harvard University Press.

Hua, X. 2016. The impact of seasonality on niche breadth, distribution range and species richness: a theoretical exploration of Janzen's hypothesis. Proceedings of the Royal Society B: Biological Sciences 283, 20160349.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. The American Naturalist 101, 233-249.

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A., Ricotta, C. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions 16, 65-76.

Kaspari, M. 2004. Using the metabolic theory of ecology to predict global patterns of abundance. Ecology 85, 1800-1802.

Kaspari, M., Ward, P. S., Yuan, M. 2004. Energy gradients and the geographic distribution of local ant diversity. Oecologia 140, 407-413.

Kaspari, M., Weiser, M. D. 2000. Ant activity along moisture gradients in a Neotropical forest. Biotropica 32, 703-711.

Körner, C. 2007. The use of ‘altitude’ in ecological research. Trends in Ecology & Evolution 22, 569-574.

Dunn, R. R., Guenard, B., Weiser, M. D., Sanders, N. J. 2010. Geographic gradients, in: Lach, L., Parr, C., Abbott, K. (Eds), Ant ecology. Oxford university press, pp. 38-58.

Lovett, J. 1990. Classification and status of the moist forests of Tanzania. Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 23a, 287-300.

Lovett, J. C. 1999. Tanzanian forest tree plot diversity and elevation. Journal of Tropical Ecology 15, 689-694.

Lovett, J. C., Marshall, A. R., Carr, J. 2006. Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. African Journal of Ecology 44, 478-490.

Lovett, J. C., Thomas, D. 1986. The ecology of pteridophytes in the Mwanihana Forest Reserve, Tanzania. Fern Gazette 13, 103-107.

Lovett, J. C., Wasser, S. K. 2008. Biogeography and ecology of the rain forests of eastern Africa. Cambridge University Press.

Malsch, A. K., Fiala, B., Maschwitz, U., Mohamed, M., Nais, J., Linsenmair, K. E. 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. Asian Myrmecology 2, 33-49.

Malumbres-Olarte, J., Crespo, L., Cardoso, P., Szűts, T., Fannes, W., Pape, T., Scharff, N. 2018. The same but different: equally megadiverse but taxonomically variant spider communities along an elevational gradient. Acta Oecologica 88, 19-28.

Malumbres-Olarte, J., Scharff, N., Pape, T., Coddington, J. A., Cardoso, P. 2017. Gauging megadiversity with optimized and standardized sampling protocols: A case for tropical forest spiders. Ecology and Evolution 7, 494-506.

Marshall, A. R., Lovett, J. C., White, P. C. 2008. Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. American Journal of Primatology 70, 452-462.

Marshall, A. R., Topp-Jørgensen, J. E., Brink, H., Fanning, E. 2005. Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. International Journal of Primatology 26, 127-145.

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography 18, 346-360.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher'in the tropics. Ecology Letters 12, 550-560.

McCoy, E. D. 1990. The distribution of insects along elevational gradients. Oikos 58, 313-322.

McGlynn, T. P., Fawcett, R. M., Clark, D. A. 2009. Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest. Biotropica 41, 234-240.

Munyai, T., Foord, S. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. Journal of Insect Conservation 16, 677-695.

Munyai, T. C., Foord, S. H. 2015. Temporal patterns of ant diversity across a mountain with climatically contrasting aspects in the tropics of Africa. PlosOne 10, e0122035.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Newmark, W. D. 2002. Conserving biodiversity in East African forests: a study of the Eastern Arc Mountains. Springer Science and Business Media.

Ossola, A., Nash, M. A., Christie, F. J., Hahs, A. K., Livesley, S. J. 2015. Urban habitat complexity affects species richness but not environmental filtering of morphologically diverse ants. PeerJ 3, e1356.

Oyen, K. J., Giri, S., Dillon, M. E. 2016. Altitudinal variation in bumble bee (Bombus) critical thermal limits. Journal of Thermal Biology 59, 52-57.

Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F. 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nature Communications 7, 13736.

R Core Development Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18, 200-205.

Romdal, T. S., Rahbek, C. 2009. Elevational zonation of afrotropical forest bird communities along a homogeneous forest gradient. Journal of Biogeography 36, 327-336.

Rosenzweig, M. L., Abramsky, Z. 1993. How are diversity and productivity related? in: Ricklefs, R. E, Schluter, D. (Eds.), Species diversity in ecological communities. University of Chicago Press, pp. 52-65.

Rovero, F., De Luca, D. W. 2007. Checklist of mammals of the Udzungwa Mountains of Tanzania. Mammalia 71, 47-55.

Rovero, F., Marshall, A. R., Jones, T., Perkin, A. 2009. The primates of the Udzungwa Mountains: diversity, ecology and conservation. Journal of Anthropological Sciences 87, 93-126.

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A., Tattoni, C. 2017. Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodiversity and Conservation 26, 1103-1119.

Rovero, F., Struhsaker, T. T., Marshall, A. R., Rinne, T. A., Pedersen, U. B., Butynski, T. M., Ehardt, C. L., Mtui, A. S. 2006. Abundance of diurnal primates in Mwanihana forest, Udzungwa Mountains, Tanzania. International Journal of Primatology 27, 675-697.

Sanders, D., Nickel, H., Grützner, T., Platner, C. 2008. Habitat structure mediates top–down effects of spiders and ants on herbivores. Basic and Applied Ecology 9, 152-160.

Sanders, N. J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography 25, 25-32.

Sanders, N. J., Lessard, J. P., Fitzpatrick, M. C., Dunn, R. R. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16, 640-649.

Sanders, N. J., Moss, J., Wagner, D. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12, 93-102.

Schöning, C., Moffett, M. W. 2007. Driver ants invading a termite nest: why do the most catholic predators of all seldom take this abundant prey? Biotropica 39, 663-667.

Stanley, W. T., Hutterer, R. 2007. Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. Acta Theriologica 52, 261-275.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. The American Naturalist 140, 893-911.

Stork, N. E., Grimbacher, P. S. 2006. Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. Proceedings of the Royal Society B: Biological Sciences 273, 1969-1975.

Szewczyk, T., McCain, C. M. 2016. A systematic review of global drivers of ant elevational diversity. PlosOne 11, e0155404.

Tittensor, D. P., Worm, B. 2016. A neutral-metabolic theory of latitudinal biodiversity. Global Ecology and Biogeography 25, 630-641.

Wang, J., Meier, S., Soininen, J., Casamayor, E. O., Pan, F., Tang, X., Yang, X., Zhang, Y., Wu, Q., Zhou, J. 2017. Regional and global elevational patterns of microbial species richness and evenness. Ecography 40, 393-402.

Ward, P. 2000. Broad-scale patterns of diversity in leaf litter ant communities, in: Agosti, D., Majer J. D., Alonso, L. E., Schultz, T. R. (Eds), Ants; Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, pp. 99-121.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J. A., Harrison, S. P. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13, 1310-1324.

Wiens, J. J., Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology Evolution and Systematics 36, 519-539.

Wiescher, P. T., Pearce-Duvet, J. M., Feener, D. H. 2012. Assembling an ant community: species functional traits reflect environmental filtering. Oecologia 169, 1063-1074.

Willig, M. R., Kaufman, D. M., Stevens, R. D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34, 273-309.

Xiong, W., Li, J., Chen, Y., Shan, B., Wang, W., Zhan, A. 2016. Determinants of community structure of zooplankton in heavily polluted river ecosystems. Scientific Reports 6, 22043.

Zilihona, I. J., Nummelin, M. 2001. Coleopteran diversity and abundance in different habitats near Kihansi waterfall, in the Udzungwa Mountains, Tanzania. Biodiversity and Conservation 10, 769-777.

CHAPTER 3: What drives ant beta diversity along the Udzungwa mountains, species turnover or richness differences?

Abstract

Disentangling the role of deterministic and neutral processes in structuring communities has gained considerable attention. Recent studies have suggested that the partitioning of beta diversity, which is the variation in species composition between two sites, into species turnover and richness differences can provide appreciable insights on the importance of these processes in structuring communities. Here, we test the relative role of distance and the environment in structuring ant assemblages along the Udzungwa Mountains in Tanzania. A standardized survey using pitfall sampling was conducted across five elevational transects which were at a distance of 0.1, 1, 20 and 174 km from the first one. Sites within transects were at three target elevations which corresponded to three forest types (lowland, 300-800 m a.s.l; sub-montane, 800-1400 m a.s.l; montane, 1400-1500 m a.s.l). Beta diversity was influenced by both elevational distance (m.a.s.l) and geographic distance (km). Dispersal limitations did not play a significant role in structuring ant composition between sites. It also did not explain variation in the two beta diversity components; species turnover and richness differences, suggesting that historical processes or biotic interactions structure ant communities with distance. Across elevations, species turnover increased with elevation while richness differences decreased with elevation. The latter elucidates the role of species replacement in structuring ant communities along an elevational gradient and that of temperature acting as an environmental filter in structuring ant compositions.

Key words: beta diversity, elevational gradient, species turnover, richness differences, biodiversity, ants (Hymenoptera; Formicidae), Udzungwa Mountains

3.1 Introduction

Beta diversity is a central concept in community ecology. It is defined as the extent of change in community composition between sites (Whittaker, 1960). It is commonly referred to as the variation in species composition between two sites (Legendre et al., 2005; Baselga, 2010; Kraft et al., 2011; Hu et al., 2018). It allows for the identification of processes that structure community assemblages (Kraft et al., 2011) and reveals how communities respond to the influence of climate change, environmental gradients and anthropogenic activities (Vellend et al., 2007; Anderson et al., 2011; Leprieur et al., 2011).

There are multiple approaches of quantifying beta diversity (Koleff et al., 2003; Baselga, 2010; Anderson et al., 2011; Podani and Schmera, 2011; Carvalho et al., 2012). However, it is the partitioning of beta diversity into two process-based components (species turnover and richness differences/nestedness) that has proven both important and useful in describing beta diversity patterns and the different mechanisms that control how community assemblages are structured (Legendre et al., 2009; Baselga, 2010; Carvalho et al., 2012; Foord and Dippenaar-Schoeman, 2016; Soininen et al., 2018). The latter is particularly important because understanding the relative importance of these two components of beta diversity gives insight on which processes drive beta diversity as well as how best to conserve specific sites/habitats of a given ecosystem (Socolar et al., 2016).

Baselga (2010) proposed the first methodological and conceptual framework, where he partitioned beta diversity into species turnover and nestedness. Species turnover being species replacement between communities. It is when species that exist in one site are replaced by different species in the next site (Bishop et al., 2015; Socolar et al., 2016; da Silva et al., 2018) as a result of environmental filtering as well as spatial and historical constraints (Qian et al., 2005; da Silva et al., 2018). Nestedness on the other hand, is the loss or gain of species between communities (Gaston, 2000). It is a result of one species assemblage being a

subset of another and is a reflection of how many habitats are available to species or are occupied at different sites (Baselga, 2010; Legendre, 2014; Soininen et al., 2018). However, Carvalho et al. (2012) suggested that nestedness is a special case of an ordered pattern of differences in species richness and there is no unequivocal way to measure it (Legendre, 2014). Therefore, a second framework partitioning beta diversity into species turnover and richness differences was proposed (Podani and Schmera, 2011; Carvalho et al., 2012). Richness differences is the loss or gain of species causing richness differences between sites. It is a result of dispersal limitation, colonization and selective extinction (Novotny and Weiblen, 2005; Urban et al., 2006; Ulrich et al., 2009) and like nestedness, it is a reflection of available niches and is due to processes that result in species thinning which cause nestedness (Legendre, 2014). This framework does not over emphasize the role of species turnover, and therefore gives the best estimate of biodiversity patterns and the processes structuring them (Carvalho et al., 2012). Changes in biodiversity across elevational gradients have been of major ecological interest, however, little is known about beta diversity patterns and their drivers across these gradients (Qian and Ricklefs, 2012; Tello et al., 2015). This is unwarranted as beta diversity captures the dynamic nature of diversity regulation better than the alpha diversity (Wang et al., 2012; Hu et al., 2018; Soininen et al., 2018). It has the potential to illuminate the different processes associated with elevation that structure community assemblages (Kraft et al., 2011), to reflect the relationships between local and regional diversity (Tello et al., 2015) and consequently inform regional conservation planning (Legendre et al., 2005; Angeler, 2013; Socolar et al., 2016).

Studies that partition beta diversity into turnover and richness differences show that the contribution of these components vary along gradients and that species turnover often contributes more to total beta diversity than richness differences (Tonial et al., 2012; Foord and Dippenaar-Schoeman, 2016; Heino et al., 2019). These patterns may be as a result of numerous

processes such as the effect of environmental conditions, dispersal limitation and species interactions (Soininen et al., 2007; Baselga, 2010; Gilman et al., 2010). They may also be a result of a gradients disturbance history, vegetation structure and range sizes (Vasconcelos et al., 2000; Kaspari et al., 2008; Hua, 2016).

It is evident that we lack studies that partition beta diversity components along both latitudinal and elevational gradients hence our understanding of the processes that govern it is limited. There are few studies (if any) with a rigorous study design that accounts for the short comings of most beta diversity studies; which are low replication, short elevational extents and the lack of within elevation replication (Kraft et al., 2011; Wang et al., 2012; Tello et al., 2015). The current study uses a sampling method that accounts for beta diversity along elevational transects, and at different geographic distances within each elevation zone. Here we aim to describe patterns of beta diversity and establish the role of elevation and geographic distance in structuring ant assemblages and how they affect species turnover and richness differences. We used ants as a model organism because they are indicator species, they occupy all terrestrial habitats and can be identified to species level (Andersen and Majer, 2004).

The Udzungwa mountains are a biodiversity hotspot threatened by climate change, land degradation and consequently biodiversity loss (Myers et al., 2000). The lowland forests were converted, leaving the mountain ranges as islands which has contributed to their high level of plant and mammal endemism (Lovett and Congdon, 1989; Lovett, 1990; Lovett and Wasser, 2008). However, anthropogenic activities continue to threaten these forests, and climate change is likely to drive species at highest elevations to extinction. We found that that ant species richness declines with increasing elevation and that different ant assemblages on these mountains are associated with its three forest types (lowland, sub-montane and montane forest) (chapter 2). It is therefore important to measure the extent of compositional change between

sites and reveal the processes that structure them, in order to better understand how ant communities are structured along elevational gradients and possibly how best to conserve them. We therefore hypothesize that (1) richness differences will contribute more to overall beta diversity than species turnover between sites because of ants limited ability to disperse long distances and (2) ant assemblages along elevation will be structured by both richness differences and species turnover as the elevational zones are close to each other but temperature acts as a barrier because it is different in each elevational zone. We predict that (1) species loss will increase with increasing geographic distance because ants will not be able to disperse long distances resulting in high richness differences, making dispersal limitations the main driver of the variation between sites. (2) The reported decrease in temperature with increasing elevation (Malumbres-Olarte et al., 2018) will limit the replacement of species in new sites as ants are thermophilic and are not adapted to live in cold environments (Kaspari and Weiser, 2000), making environmental conditions the main driver of variation between elevational distances.

3.2 Methods and Materials

Study Sites Description

The Udzungwa Mountains (7.82° S, 36.70° E) are a major center of mammal and plant endemism. It is widely recognized for its outstanding biodiversity and high endemicity (Rovero and De Luca, 2007). The Udzungwa Mountains form the largest block of the Eastern Arc Mountains (Burgess *et al*., 2007) covering 10 000 km^2. Their long-term climatic stability has made them endure through millions of years (Lovett and Wasser, 2008). The altitude ranges from 200 to 2500 m a.s.l. with heterogeneous habitats. It has lowland rainforest (300–800 m a.s.l.); submontane rainforest (700–1400 m a.s.l.); montane rainforest (1400–1800 m a.s.l.); and mountain bamboo forest (1800 m a.s.l.) as described by Shangali et al., (1998). The climate in

the Udzungwa Mountains is variable and it receives rainfall between 2000-3000 mm per year, due to the influence of the Indian Ocean (Lovett *et al*., 2006; Rovero *et al*., 2009; Mumbi *et al*., 2008, Rovero *et al*., 2017). It has a heavy rainy reason between March and May, and a light rainy season between November and February (Lovett and Thomas, 1986).

The Udzungwa Mountains has a gradient in forest types (Lovett et al., 2006; Rovero et al., 2017). It is covered by deciduous miombo (*Brachystegia* spp) in the lowland (300 m a.s.l) and by a mosaic of bamboo (*Sinarundinaria alpina*) and *Hagenia abyssinica* in the evergreen montane rainforest (2400 m a.s.l) (Table 1) (Lovett and Wasser, 2008; Rovero et al., 2017). In 1992 one fifth of the mountain was protected as the Udzungwa Mountain National Park (Rovero et al., 2009) where our study was conducted.

Ant sampling

Five elevational transects were be set up, each with a 50 m x 50 m square plot at each of the three target elevations (300-800, 800-1400 and 1200-1500 m a.s.l.) which correspond to three different forest types (lowland forest, sub-montane forest and montane forest, respectively, Table 2.1)) (Lovett, 1999). The five transects were separated by 0.1, 1, 20 and 175 km between the first and the remaining transects.

Twelve pitfall samples (where each sample consisted of four pitfall traps) were collected, as part of the application of the COBRA-TF sampling protocol (Malumbres-Olarte et al., 2017) in October–November 2014. They were partly filled with preservative solution (propylene glycol) and a few drops of liquid soap to break surface tension and sheltered using lids on stilts about 2-3 cm above the ground. The traps were left in the field for 2 weeks.

Samples were washed in the laboratory and stored in 96% ethanol. Ants were identified to genus level using Fisher and Bolton (2016) and then identified to species level where possible using online databases; *viz.* AntWiki (http://www.antwiki.org/) and AntWeb (http://antweb.org/).

and then assigned to morphospecies. Voucher species are held in the Zoological Museum of the Natural History Museum of Denmark, Copenhagen, Denmark.

Data analysis

Data was analysed using the R programming environment version 3.4.1 (R Core Team, 2017). Beta diversity was partitioned as proposed by Carvalho et al (2013) to determine the relative role of species replacement and richness differences in generating beta diversity. Beta diversity was measured as the Jaccard index into two additive components, difference due to turnover and difference due to species loss/gain. The measures do not overestimate the role of species turnover (Carvalho et al., 2012) and are not sensitive to undersampling (Cardoso et al., 2009). The observed metrics were then compared with those expected under a random model of community assembly in order to identify the processes that drive beta diversity patterns. One thousand random assemblages whose species occurrence frequency and sample species richness were maintained while species occurrence was shuffled across sites, were generated using the independent swap method of the 'randomizeMatrix' function in the 'picante' package (Kembel et al., 2010). We then calculated the standardised effect sizes (SES) of the observed measures as a function of mean and standard deviation of the null distribution (Bishop et al., 2015). SES values > 1.96 and < - 1.96, are significantly larger or smaller than expected. Multiple regressions were performed to model the response of the three beta diversity metrics and their SES to distance and elevational distance using the function 'lm' in the package 'lme4' (Bates et al., 2013). A quadratic term was included for the observed metrices to account for nonlinear responses of geographic and elevational distance in diversity. Model predictions were then visualized using the 'ggplot2' function (Wickham, 2016).

Community composition

Variation in community composition was analysed using the latent variable modelling. This is a Bayesian model-based approach that uses a set of underlying latent variables to account for residual correlation among species in order to explain community composition. The Bayesian model-based approach accounts for overdispersion in data without confounding location with dispersion by offering the option to adjust the distribution family to for example “poisson” or “negative binomial” (Hui, 2016). Model-based unconstrainted ordination was performed using the ‘boral’ package. Ant communities were modelled with two latent variables and negative binomial distribution to visually represent similarities between communities at sites.

3.3 Results

Observed patterns

Distance explained a significant amount of variation in beta diversity. There is a polynomial relationship between distance (km) and overall beta diversity in the lowland forest, however, distance seems to play a limited role in structuring ant communities as neither species turnover nor richness differences significantly explain variation in species composition (Table 3.1). There is a significant linear increase in total beta diversity explained by species turnover at intermediate distances (10 km) and richness differences at furthest distances (100 km) (Table 3.1). The latter suggests that distance does not affect beta diversity in the lowland forest while richness differences structure ant communities in the sub-montane forest and species turnover structures ant communities at intermediate distance and richness differences structure ant communities at furthest distances in the montane forest.

There is a linear increase in total beta diversity with elevational differences (Figure 3.1) and both species turnover and richness differences contribute significantly in explaining the variation in total beta diversity (Table 3.1). We observed a polynomial relationship between species turnover and elevational differences while we observed a linear relationship between

richness differences and elevational differences (Table 3.1). Species turnover shows a convex relationship while richness differences show a concave relationship with elevational differences (Figure 3.2). The latter suggest that species turnover structures ant communities at intermediate elevational differences (500 m.a.s.l) while richness differences structures them at high elevational differences. The role of richness differences becomes more important in structuring ant communities with increasing elevational distance.

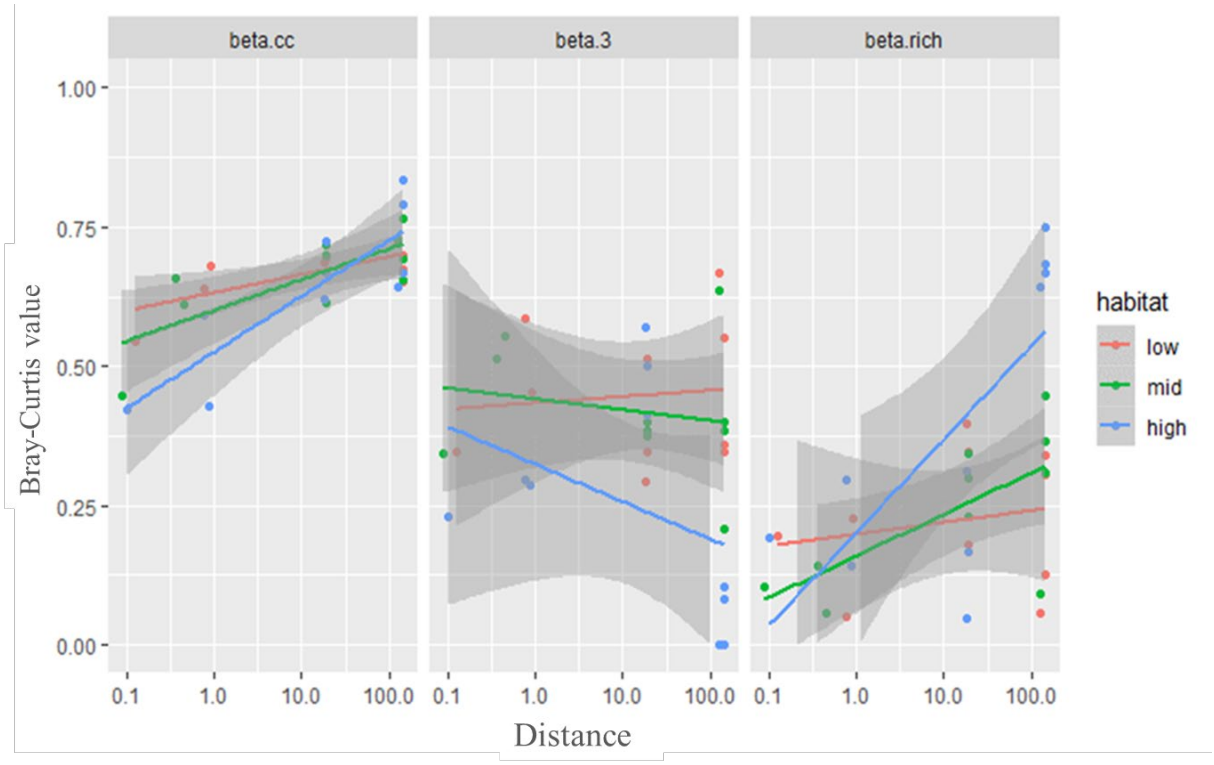


Figure 3. 1: The contribution of total beta (Bray-Curtis), species turnover ($Beta_3$) and richness differences ($Beta_{rich}$) to beta diversity patterns between sites in the lowland (low), sub-montane (mid) and montane (high) forests of the Udzungwa mountains.

Table 3. 1: Results of multiple regressions for the relationship between total beta diversity, turnover and species loss with distance and elevation.

	Low	Medium	High	Elevation
	Jaccard index			
Intercept	0.65***	0.66***	0.5***	0.73***
Distance	0.034**	0.103*	0.11**	0.1***
$Distance^2$	-0.006*			
$Distance^3$				
R2- adjusted	0.75	0.53	0.68	0.64
	Differences due to turnover			
Intercept	0.43***	0.46***	0.5***	0.54***
Distance	0.002	-0.08	-0.36	0.14*
$Distance^2$			-0.35***	-0.059**
$Distance^3$			-0.14**	-0.06.
R2- adjusted	-0.11	-0.08	0.88	0.18
	Differences due to species loss			
Intercept	0.22*	0.24*	0.15*	0.25**
Distance	0.02	0.09*	0.15.	0.08***
$Distance^2$			0.34**	
$Distance^3$			0.13*	
R2- adjusted	-0.08	0.4	0.89	0.24

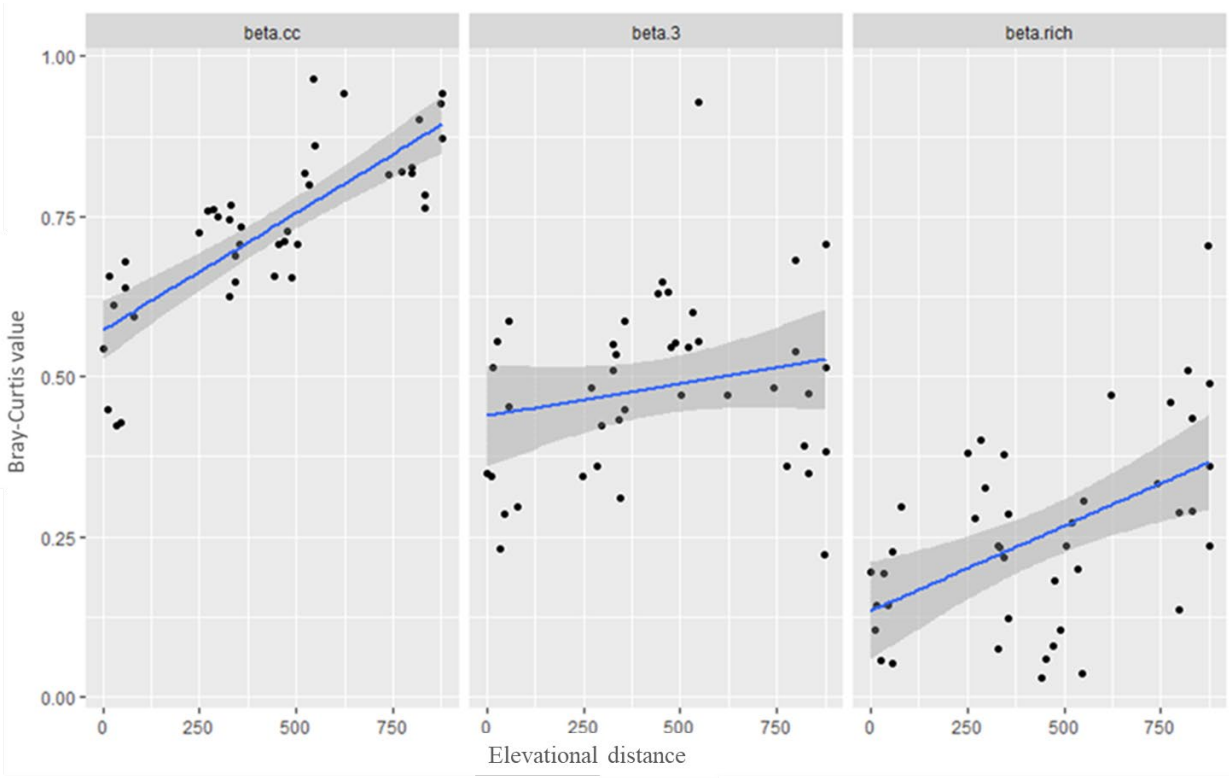


Figure 3. 2: The contribution of total beta ($Beta_{jac}$), species turnover ($Beta_3$) and richness differences ($Beta_{rich}$) to beta diversity patterns along an elevational transect on the Udzungwa mountains.

Standardized patterns

The standardised effect sizes for overall beta diversity slightly increase with distance in the lowland, sub-montane and montane forest (Figure 3.3). Standardised species turnover increases from less than expected to greater than expected with increasing distance in the sub-montane forest, while it slightly increases in the lowland and montane forest (Figure 3.3). There is a slight decrease in the standardised richness differences in all three forest types. The findings suggest that, although the relationship between distance and beta diversity is small, distance does influence the rate of turnover and that species replacement and species loss/gain does not play a role in explaining beta diversity patterns between sites that are different in distances from each other across all three habitat types (Table 3.2).

The standardised effect sizes for overall beta diversity increase with increasing elevational distance (Figure 3.4). Overall beta diversity is lower than expected at small elevational distances and is higher than expected at larger elevational distances. Standardised species turnover increases with increasing elevational distance while standardised richness differences decrease with increasing elevational distance (Figure 3.4). These results suggest that turnover is significantly influenced by elevational distance. The role of richness differences in structuring ant communities decreases with elevation, while that of species turnover increases with elevation suggesting that species turnover is important in structuring ant communities along an elevational gradient.

Table 3. 2: Results of multiple regressions for the SES relationship between total beta diversity, turnover and species loss with distance.

	Low	Medium	High	Elevation
	Jaccard index			
Intercept	0.520	0.586	0.830	8.28e-09***
Distance	0.292	0.409	0.791	2.52e-10***
R2- adjusted	0.29	-0.03	-0.12	0.63
	Differences due to turnover			
Intercept	0.552	0.0176*	0.819	5.96e-09***
Distance	0.308	0.1226	0.779	1.89e-10 ***
R2- adjusted	0.02	0.19	-0.11	0.65
	Differences due to species loss			
Intercept	0.55	0.585	0.821	8.01e-09 ***
Distance	0.309	0.402	0.775	2.84e-10***
R2- adjusted	0.02	-0.03	-0.11	0.63

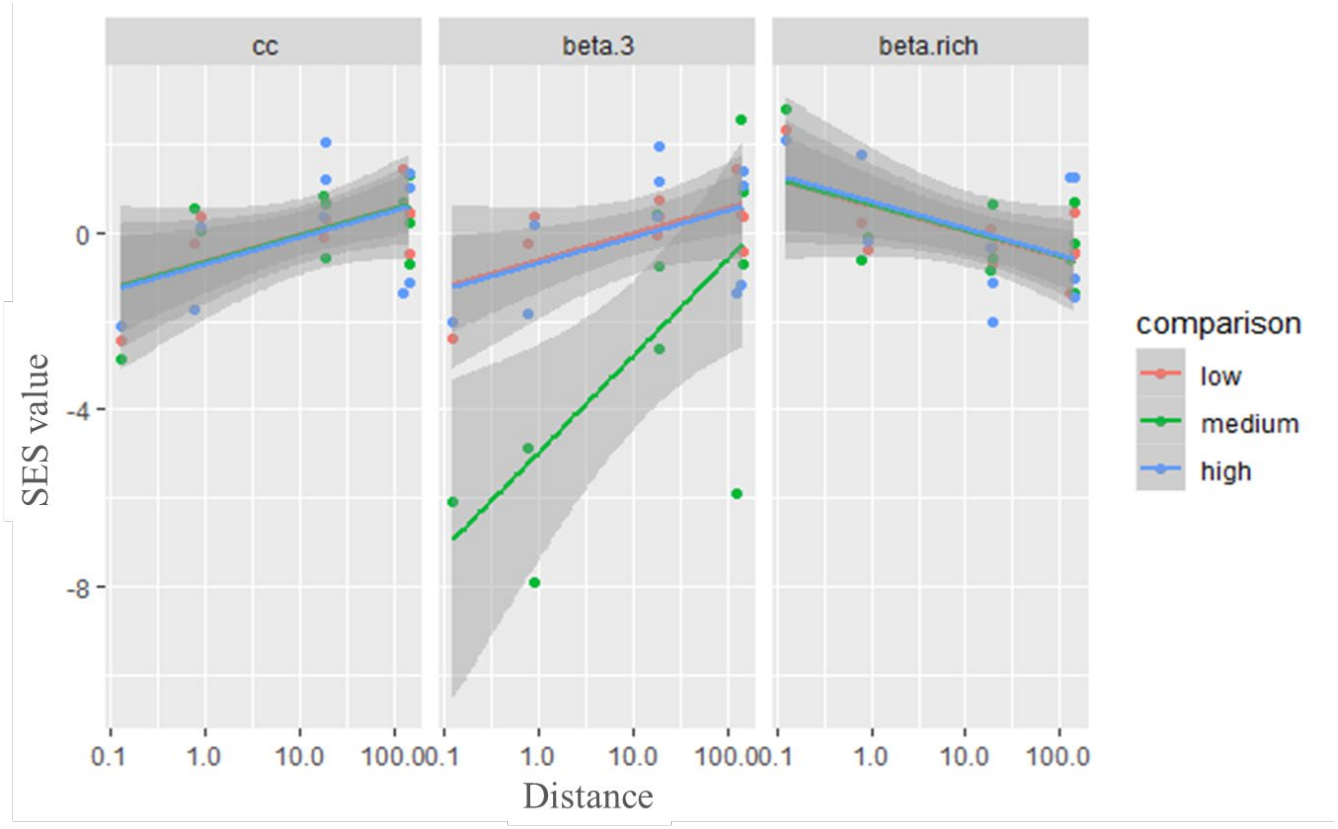


Figure 3. 3: The SES contribution of total beta (Bray-Curtis), species turnover ($Beta_3$) and richness differences ($Beta_{rich}$) to beta diversity patterns between sites in the lowland (low), sub-montane (medium) and montane (high) forests of the Udzungwa mountains.

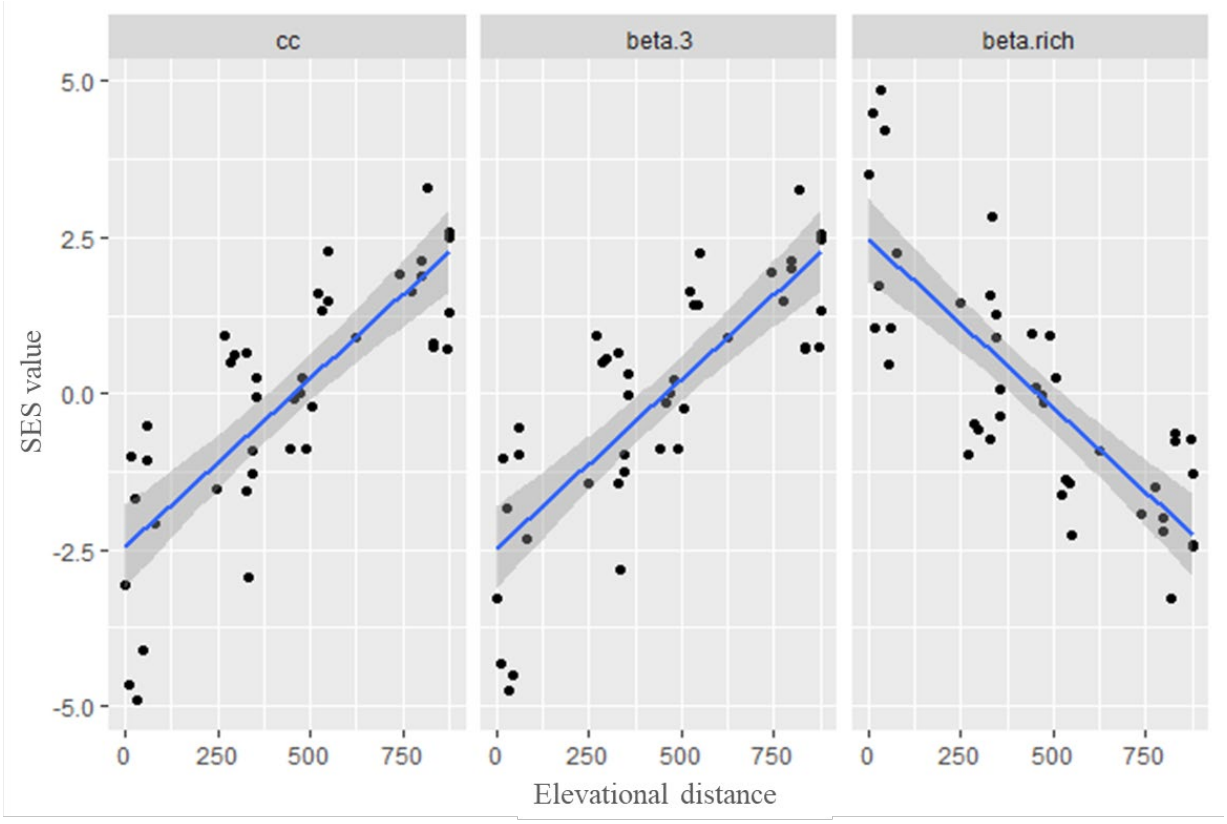


Figure 3. 4: The SES contribution of total beta ($Beta_{jac}$), species turnover ($Beta_3$) and richness differences ($Beta_{rich}$) to beta diversity patterns along an elevational transect on the Udzungwa mountains.

Community similarity

There are three distinct assemblages along the Udzungwa mountains which correspond to the three elevations (lowland, sub-montane and montane) (Figure 3.3). The sub-montane ant communities are intermediate between montane and lowland sites (Figure 3.3). Fifteen species were associated with all three forest types. Forty-one species were restricted to the lowland, twelve occurred in the sub-montane and thirteen restricted to the montane forest. The similarity or dissimilarity between these assemblages seem to be affected by both distance (km) and elevational distance (Table 3.1; Figure 3.3).

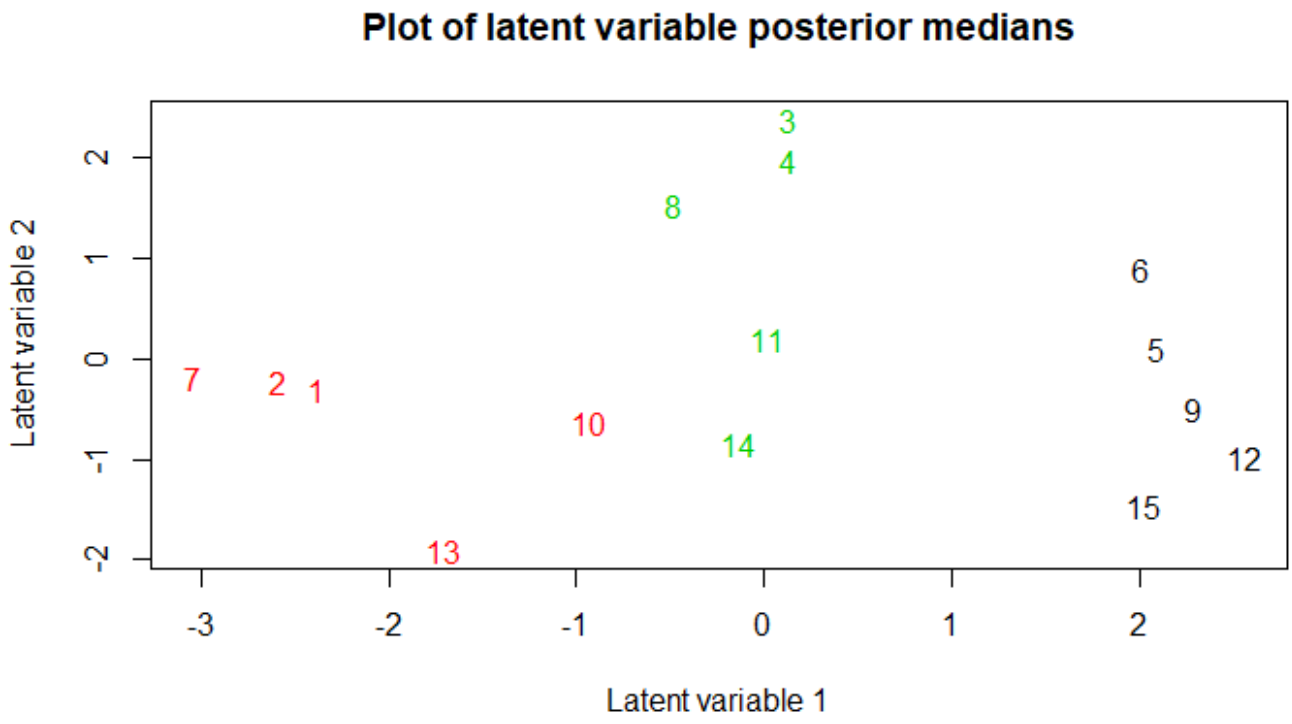


Figure 3. 5: Plot of community similarity based on ant species sampled in three forests types: lowland (red), sub-montane (green), montane (black) in the Udzungwa Mountains, Tanzania.

3.4 Discussion

This study provides insight into the processes that structure ant communities along the Udzungwa mountains, Tanzania. To the best of our knowledge, it is the first to measure taxonomic beta diversity along an elevational gradient given a sampling design that accounts for turnover with an increase in elevation (600-1500 m.a.s.l) as well as an increase in geographic distance (0.1-175 km) for African ants. Bishop et al. (2015) measured ant species and functional beta diversity across the Drakensberg mountains, giving insight on processes that may control elevational patterns, while Foord and Dippenaar-Schoeman (2016) studied beta diversity for spiders along the Cederberg mountains. However, the latter studies lack comparison of transects at different distances (Wang et al., 2012; Tello et al., 2015).

Sites at the same elevation would be expected to have similar environmental conditions, particularly temperature, no matter the distance between them considering that they are at the same latitude. The latter, suggests that beta diversity would depend exclusively on dispersal limitation and thus increase with increasing geographic distance (Vasconcelos et al., 2010). The SES results, however, show that ant compositions are not strongly driven by dispersal limitation as there was only a slight variation in beta diversity with increasing distance. The SES results also show that distance does not explain much of the variation in both beta diversity components (species turnover and richness differences) even though species turnover appeared to be less than expected by chance and richness differences larger than expected by chance with increasing distance. The latter suggests the role of biotic interactions (e.g. predation, competition and mutualism) in structuring ant communities with varying geographic distance, which are some of the most important factors that structure communities (Gilman et al., 2010) as they have the potential to modify resource availability or local abiotic conditions (Boulangeat et al., 2012). The similar environment within same elevations may have also selected for a similar composition of ants and stochastic factors such as random colonization, extinction and ecological drift may have contributed to the structuring of ant communities with distance (Chase and Myers, 2011).

Elevation significantly affected beta diversity patterns, emphasizing the role of environmental filtering in structuring ant communities. The observed overall beta diversity increased with increasing elevation, showing that turnover is highest in high elevations. This finding contradicts Kraft et al. (2011) and Tello et al. (2015) who found that beta diversity decreases towards high elevations but was, however, similar to Bishop et al. (2015), who reported an increase in beta diversity with increasing elevation, which was largely driven by species turnover.

In this study the role of species turnover in structuring ant communities increased with increasing elevation, suggesting that species replacement is the main driver of ant communities along an elevation gradient. Richness differences on the other hand decreased with elevation. Sites that are very close to each other tend to have the same species and only really differ in terms of richness while sites that are distant elevational-wise have very different species and don't differ much in the number of species perhaps owing to the harsh temperature conditions only allowing for adapted species to establish and survive at high elevations, trading off large population sizes for traits suitable for survival.

Similar to Bishop et al. (2015) ants on the Udzungwa mountains tend to be specialized to certain elevations and not the entire gradient emphasising the role temperature as a strong predictor of ant communities along elevational gradients. In the tropics, species are known to have narrow temperature ranges (Janzen, 1967). The latter therefore, makes mountain passes effective barriers of dispersal as species with narrow temperature ranges at one elevation have low fitness to move to another elevation (Janzen, 1967). This also limits elevational ranges of tropic species and promotes speciation along mountain slopes (Moritz et al., 2000; McCain, 2009; Hua, 2016).

Three ant species assemblages associated with each target elevation were observed. The low and mid-elevation assemblages were almost similar while the high elevation assemblage was distinct, perhaps owing to reduced effective dispersal of species as a result of narrow temperature and elevational ranges. Species restricted to the three target elevations seem to have narrow temperature and elevational ranges.

In conclusion, this study reveals that beta diversity is affected by elevational distance (more pronounced) and distance (slightly less pronounced). Beta diversity did not vary much with increasing geographic distance, suggesting that dispersal limitation play a minimal role in structuring ant communities between sites therefore emphasizing the role of the environment

and not dispersal in explaining variation in ant communities at different geographic distances. Along an elevational gradient, species turnover structed ant communities at high elevations, while richness differences structured ant communities at low elevation, perhaps owing to temperature selectively filtering which species can establish and survive at each different elevation. These results suggest that temperature is very important in structuring ant communities along the Udzungwa mountains and that complementarity between sites is maximized by choosing sites that are at different elevations.

References

Andersen, A. N., Majer, J. D. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2, 291-298.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14,19-28.

Angeler, D. G. 2013. Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. Diversity and Distributions 19, 772-781.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134-143.

Bates, D., Maechler, M., Bolker, B., Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1(7), 1-23.

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., Parr, C. L. 2015. Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography 42, 1776-1786.

Boulangeat, I., Gravel, D., Thuiller, W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecology Letters 15, 584-593.

Bruna, E. M., Izzo, T. J., Inouye, B. D., Uriarte, M., Vasconcelos, H. L. 2011. Asymmetric dispersal and colonization success of Amazonian plant-ants queens. PlosOne 6, e22937.

Burgess, N., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldså, J., Howell, K. M., Kilahama, F. B., Loader, S. P., Lovett, J. C., Mbilinyi, B., Menegon, M., 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation 134(2), 209-231.

Cardoso, P., Borges, P. A., Veech, J. A. 2009. Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. Diversity and Distributions 15(6), 1081-1090.

Carvalho, J. C., Cardoso, P., Gomes, P. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography 21, 760-771.

Carvalho, J. C., Cardoso, P., Borges, P. A., Schmera, D., Podani, J. 2013. Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. Oikos 122(6), 825-834.

Chase, J. M., Myers, J. A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical transactions of the Royal Society B: Biological Sciences 366(1576), 2351-2363

da Silva, P. G., Lobo, J. M., Hensen, M. C., Vaz-de-Mello, F. Z., Hernández, M. I. 2018. Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. Diversity and Distributions 24, 1277-1290.

Foord, S. H., Dippenaar-Schoeman, A. S. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. Journal of Biogeography 43, 2354-2365.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405,220.

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., Holt, R. D. 2010. A framework for community interactions under climate change. Trends in Ecology and Evolution 25,325-331.

Gómez, C., Espadaler, X. 2013. An update of the world survey of myrmecochorous dispersal distances. Ecography 36, 1193-1201.

Heino, J., Alahuhta, J., Fattorini, S., Schmera, D. 2019. Predicting beta diversity of terrestrial and aquatic beetles using ecogeographical variables: insights from the replacement and richness difference components. Journal of Biogeography 46, 304-315.

Hu, Y., Ding, Z., Jiang, Z., Quan, Q., Guo, K., Tian, L., Hu, H., Gibson, L. 2018. Birds in the Himalayas: What drives beta diversity patterns along an elevational gradient? Ecology and Evolution 8, 11704-11716.

Hua, X. 2016. The impact of seasonality on niche breadth, distribution range and species richness: a theoretical exploration of Janzen's hypothesis. Proceedings of the Royal Society B: Biological Sciences 283, 20160349.

Hui, F. K. 2016. boral–Bayesian ordination and regression analysis of multivariate abundance data in R. Methods in Ecology and Evolution 7(6), 744-750.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. The American Naturalist 101, 233-249.

Kaspari, M., Weiser, M. D. 2000. Ant activity along moisture gradients in a neotropical forest 1. Biotropica 32,703-711.

Kaspari, M., Yanoviak, S. P., Dudley, R. 2008. On the biogeography of salt limitation: a study of ant communities. Proceedings of the National Academy of Sciences 105, 17848-17851.

Kembel, S. W., Cowan, P.D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., Webb, C. O. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26(11), 1463-1464.

Koleff, P., Gaston, K. J., Lennon, J. J. 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72, 367-382.

Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science 333, 1755-1758.

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23, 1324-1334.

Legendre, P., Borcard, D., Peres-Neto, P. R. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75, 435-450.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.-F., He, F. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90, 663-674.

Lennon, J. J., Koleff, P., Greenwood, J., Gaston, K. J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. Journal of Animal Ecology 70, 966-979.

Leprieur, F., Tedesco, P. A., Hugueny, B., Beauchard, O., Dürr, H. H., Brosse, S., Oberdorff, T. 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology Letters 14, 325-334.

Lovett, J. 1990. Classification and status of the moist forests of Tanzania. Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg, 287-300.

Lovett, J., Congdon, T. 1989. Notes on the Ihangana Forest and Luhega Forest near Uhafiwa, Udzungwa Mountains, Tanzania. East Africa Natural History Society Bulletin 19, 30-31.

Lovett, J. C., Marshall, A. R., Carr, J. 2006. Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. African Journal of Ecology 44, 478-490.

Lovett, J. C., Wasser, S. K. 2008. Biogeography and ecology of the rain forests of eastern Africa. Cambridge University Press.

Malumbres-Olarte, J., Crespo, L., Cardoso, P., Szűts, T., Fannes, W., Pape, T., Scharff, N. 2018. The same but different: equally megadiverse but taxonomically variant spider communities along an elevational gradient. Acta oecologica 88, 19-28.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher'in the tropics. Ecology Letters 12, 550-560.

McCain, C. M., Beck, J. 2016. Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness. Global Ecology and Biogeography 25, 299-310.

McFadden, I. R., Sandel, B., Tsirogiannis, C., Morueta-Holme, N., Svenning, J. C., Enquist, B. J., Kraft, N. J. 2019. Temperature shapes opposing latitudinal gradients of plant taxonomic and phylogenetic β diversity. Ecology Letters 22(7), 1126–1135.

Moritz, C., Patton, J., Schneider, C., Smith, T. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology and Systematics 31, 533-563.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Novotny, V., Weiblen, G. D. 2005. From communities to continents: Beta diversity of herbivorous insects. Annales Zoologici Fennici 42(4), 463-475

Podani, J., Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. Oikos 120, 1625-1638.

Qian, H., Ricklefs, R. E. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. Global Ecology and Biogeography 21, 341-351.

Qian, H., Ricklefs, R. E., White, P. S. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. Ecology Letters 8, 15-22.

Qin, H., Dong, G., Zhang, F. 2019. Relative roles of the replacement and richness difference components of beta diversity following the ecological restoration of a mountain meadow, north China. Ecological Informatics 52, 159-165.

R Core Development Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rádková, V., Syrovátka, V., Bojková, J., Schenková, J., Křoupalová, V., Horsák, M. 2014. The importance of species replacement and richness differences in small-scale diversity

patterns of aquatic macroinvertebrates in spring fens. Limnologica-Ecology and Management of Inland Waters 47, 52-61.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18, 200-205.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. The American Naturalist 149, 875-902.

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A., Tattoni, C. 2017. Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodiversity and Conservation 26, 1103-1119.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., Edwards, D. P. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31, 67-80.

Soininen, J., Heino, J., Wang, J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Global Ecology and Biogeography 27, 96-109.

Soininen, J., McDonald, R., Hillebrand, H. 2007. The distance decay of similarity in ecological communities. Ecography 30, 3-12.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. The American Naturalist 140, 893-911.

Tello, J. S., Myers, J. A., Macía, M. J., Fuentes, A. F., Cayola, L., Arellano, G., Loza, M. I., Torrez, V., Cornejo, M., Miranda, T. B. 2015. Elevational gradients in β-diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. PlosOne 10, e0121458.

Tonial, M. L. S., Silva, H., Tonial, I. J., Costa, M. C. d., Silva Júnior, N. J. d., Diniz-Filho, J. A. F. 2012. Geographical patterns and partition of turnover and richness components of beta-diversity in faunas from Tocantins river valley. Brazilian Journal of Biology 72, 497-504.

Ulrich, W., Almeida-Neto, M., Gotelli, N. J. 2009. A consumer's guide to nestedness analysis. Oikos 118, 3-17.

Urban, M. C., Skelly, D. K., Burchsted, D., Price, W., Lowry, S. 2006. Stream communities across a rural–urban landscape gradient. Diversity and Distributions 12, 337-350.

Vasconcelos, H., Vilhena, J., Caliri, G. 2000. Responses of ants to selective logging of a central Amazonian forest. Journal of Applied Ecology 37, 508-514.

Vasconcelos, H. L., Vilhena, J. M., Facure, K. G., Albernaz, A. L. 2010. Patterns of ant species diversity and turnover across 2000 km of Amazonian floodplain forest. Journal of Biogeography 37, 432-440.

Vellend, M., Verheyen, K., Flinn, K. M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B. J., Bellemare, J., Honnay, O. 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. Journal of Ecology 95, 565-573.

Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., Shen, J. 2012. Patterns of elevational beta diversity in micro-and macroorganisms. Global Ecology and Biogeography 21, 743-750.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30, 279-338.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer.

CHAPTER 4: CONCLUSION AND RECOMMENDATION FOR FURTHER RESEARCH

4.1 Introduction

Tropical rainforests are the most diverse terrestrial ecosystems on Earth (Harrison, 2005). A large proportion of their animal biomass comes from ants (Holldobler and Wilson, 1990; Brühl et al., 1999) although they are largely not understood (Longino et al., 2014). Studying ant biodiversity patterns and processes structuring them along tropical rainforests could therefore contribute to our knowledge of the processes driving their high diversity and consequently give insight on how to best conserve them. The current study specifically aimed to contribute to the knowledge of African tropical rainforests by investigating both alpha and beta ant diversity along an elevational gradient along the Udzungwa mountains.

Alpha diversity is species richness within a site (Whittaker et al., 2001). It gives a description of species diversity found along the local scale (Whittaker, 1960) while beta diversity is the variation in species composition between two sites and it operates at a regional scale (Whittaker, 1960; Whittaker, 1972). The current study investigated both alpha and beta diversity by quantifying ant diversity, documenting their diversity patterns and identifying which processes structure ant communities; whether it was species turnover or richness differences. By so doing, a comprehensive reference was built for protecting regional biodiversity (Anderson et al., 2011; Socolar et al., 2016).

4.2 Revisiting the aims and objectives

The first aim of the study was to describe ant diversity patterns along an elevational gradient in the Udzungwa Mountains and assess how ant assemblages vary with the three forest types along the mountain ranges. The current study reported a decline of ant species richness with

increasing elevation and therefore once again observing the most documented biodiversity patterns along elevational gradients. The latter is not surprising because ants are thermophilic organisms (Kaspari and Weiser, 2000), and their limited tolerance to the cold may have caused their decline as temperature also decreases with increasing elevation (Dunn et al., 2010; Malumbres-Olarte et al., 2018). Three different assemblages were found on these mountains. The lowland had a distinct assemblage owing to the narrow elevational ranges tropical species have, while the sub-montane and montane forest shared some species. The findings of this study suggest that ants are niche conservative (Wiens and Graham, 2005). The latter suggests that ants have limited tolerance to the cold limits their ability to disperse from one elevation to the next (Wiens et al., 2010). In the context of climate change, ants of the Udzungwa mountains would move up the mountain in search of suitable conditions, while montane species face the risk of being pushed to extinction.

The second aim of the study was to understand the processes that drives ant communities by investigating beta diversity patterns and the role of niche and dispersal processes in structuring ant communities within an elevation and along the Udzungwa mountains ranges. Findings show that beta diversity is affected by both distance and elevation. Beta diversity increased with increasing elevation and increasing distance. SES results suggest that the role of species turnover in structuring ant communities increases with distance and elevation, while that of richness differences decreases with both distance and elevation. Species turnover is important in structuring ant communities along elevational distance suggesting that ants are locally adapted to environmental conditions of the different elevation zones while dispersal limitations play a limited role in structuring ant communities with increasing distance, suggesting that biotic interactions structure ant communities.

4.3 Contributions of the study

This study is the first to document ant biodiversity patterns and their possibly drivers along the Udzungwa mountains in Tanzania. The Udzungwa Mountains ranges are a biodiversity hotspot well known for mammal and plant endemism (Rovero et al., 2009). Invertebrates, however, are highly successful and diverse group which are largely understudied across the region. This study therefore contributes to the knowledge of a dominant terrestrial invertebrate group, ants (Hymenoptera: Formicidae), on these mountains and African tropics in general (Botes et al., 2006; Munyai and Foord, 2012; Bishop et al., 2015). It has revealed another decline in tropical ant species richness with increasing elevation (Brühl et al., 1999; Malsch et al., 2008; Longino et al., 2014). The high diversity as well as distinct assemblage associated with the lowland forest suggests that there is a high need to conserve this forest type. In fact, there is need to conserve the whole mountains as findings show that ants are niche conservative as their distribution is restricted to the forest type or elevation zone they are found in.

In order to best inform conservation planning, we must understand beta diversity patterns and the processes that structure them (Socolar et al., 2016). This study is the first to measure beta diversity patterns with a sampling method that accounts for within elevation replicates which are often lacking in most beta diversity studies. It is also one of the few studies (Carvalho et al., 2012; Foord and Dippenaar-Schoeman, 2016) to partition beta diversity into species turnover and richness differences along elevational gradients, which is particularly important in informing conservation planning. The findings of this study could be used to best inform conservation planning in the Udzungwa mountains.

4.4 Challenges

For decades, studies have been documenting biodiversity patterns and the processes that structure them. Despite this long-standing investigation, biodiversity remains unquantified in

remote areas, especially in Africa. The contribution of humankind to climate change (Hulme et al., 1999), the degradation of ecosystems (Mona et al., 2019) and the introduction of invasive species (Meineke et al., 2018) is accelerating biodiversity loss, and the latter leaves us at risk of losing biodiversity that has not been documented. Therefore, there is a great demand for quantifying biodiversity in tropical rainforests and coming up with conservation programs, especially in understudied areas.

Alpha diversity and how it is quantified is relatively well understood, however beta diversity is a little challenging. Beta diversity has multiple definitions as well as methodological concepts of quantifying it (Tuomisto, 2010; Anderson et al., 2011). Baselga (2010) and Carvalho et al. (2012) proposed the partitioning of beta diversity into species richness and richness differences/nestedness and it is indeed important as it gives insight on how to best inform conservation programs (Socolar et al., 2016).

4.5 Future possibilities

Ants are ecologically important organisms found in almost all terrestrial habitats (Folgarait, 1998). Their distribution is shaped by several mechanisms such as environmental conditions, species interactions, historical and geographical factors i.e. dispersal limitation (Dröse et al., 2019). The way these mechanisms shape communities vary with respect to the different components of diversity, as taxonomic, phylogenetic and functional diversity provide unique information on biodiversity and consequently the way in which it should be conserved (Webb et al., 2002; Cadotte et al., 2010; Cadotte et al., 2011). The current study investigated taxonomic diversity, and the next is step is understanding phylogenetic and functional processes of biodiversity and understanding the processes that shape them.

Understanding ant phylogenetic diversity and functional diversity along the Udzungwa mountains and linking it to ant taxonomic diversity can provide insight into the extent to which

communities are structured by niche processes as well as dispersal limitation (Cavender-Bares et al., 2009; Pavoine and Bonsall, 2011; Purschke et al., 2013). Phylogenetic diversity has the potential to reflect if a system faced with environmental changes can generate new evolutionary solutions or it can persist despite the changes (Forest et al., 2007; Faith, 2008) while functional diversity has the potential to reflect the functional response of species communities to environmental filters as well the communities ability to occupy functional niche space in order to optimize ecosystem functioning (Díaz et al., 2007; Cadotte et al., 2009). Therefore, future work has the potential to reveal exactly how phylogenetics and functional traits structure ant communities along the Udzungwa mountain ranges.

4.6 Final comments and summary of the conclusion

Explaining the coexistence of the diverse species assemblages found in tropical rainforests remains a challenge in tropical ecology (Harrison, 2005). Much of its biodiversity remains unquantified and biodiversity patterns understudied. This study has documented both local and beta diversity patterns as well as the role of niche and dispersal processes that structure ant communities along mountain ranges in the African tropics. It has revealed the need for conservation on these mountains and has given insight on how best to conserve the mountain's different forest types and at different distances.

References

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14, 19-28.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134-143.

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., Parr, C. L. 2015. Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography 42, 1776-1786.

Botes, A., McGeoch, M., Robertson, H., Van Niekerk, A., Davids, H., Chown, S. 2006. Ants, altitude and change in the northern Cape Floristic Region. Journal of Biogeography 33, 71-90.

Brühl, C. A., Mohamed, M., Linsenmair, K. E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology 15, 265-277.

Cadotte, M. W., Carscadden, K., Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48, 1079-1087.

Cadotte, M. W., Cavender-Bares, J., Tilman, D., Oakley, T. H. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PlosOne 4, e5695.

Cadotte, M. W., Jonathan Davies, T., Regetz, J., Kembel, S. W., Cleland, E., Oakley, T. H. 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecology Letters 13, 96-105.

Carvalho, J. C., Cardoso, P., Gomes, P. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography 21, 760-771.

Cavender-Bares, J., Kozak, K. H., Fine, P. V., Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12, 693-715.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T. M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences 104, 20684-20689.

Dröse, W., Podgaiski, L. R., Dias, C. F., de Souza Mendonça Jr, M. 2019. Local and regional drivers of ant communities in forest-grassland ecotones in South Brazil: A taxonomic and phylogenetic approach. PlosOne 14, e0215310.

Faith, D. P. 2008. Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. Conservation Biology 22, 1461-1470.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7, 1221-1244.

Foord, S. H., Dippenaar-Schoeman, A. S. 2016. The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. Journal of Biogeography 43, 2354-2365.

Forest, F., Grenyer, R., Rouget, M., Davies, T. J., Cowling, R. M., Faith, D. P., Balmford, A., Manning, J. C., Procheş, Ş., van der Bank, M. 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445, 757-760.

Harrison, R. D. 2005. Figs and the diversity of tropical rainforests. Bioscience 55, 1053-1064.

Hölldobler, B., Wilson, E. O. 1990. The ants. Harvard University Press.

Hulme, M., Barrow, E. M., Arnell, N. W., Harrison, P. A., Johns, T. C., Downing, T. E. 1999. Relative impacts of human-induced climate change and natural climate variability. Nature 397, 688-691.

Kaspari, M., Weiser, M. D. 2000. Ant activity along moisture gradients in a neotropical forest 1. Biotropica 32, 703-711.

Dunn, R. R., Guenard, B., Weiser, M. D., Sanders, N. J. 2010. Geographic gradients, in: Lach, L., Parr, C., Abbott, K. (Eds), Ant ecology. Oxford university press, pp. 38-58.

Longino, J. T., Branstetter, M. G., Colwell, R. K. 2014. How ants drop out: ant abundance on tropical mountains. PlosOne 9, e104030.

Malsch, A. K., Fiala, B., Maschwitz, U., Mohamed, M., Nais, J., Linsenmair, K. E. 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. Asian Myrmecology 2, 33-49.

Malumbres-Olarte, J., Crespo, L., Cardoso, P., Szűts, T., Fannes, W., Pape, T., Scharff, N. 2018. The same but different: equally megadiverse but taxonomically variant spider communities along an elevational gradient. Acta Oecologica 88, 19-28.

Meineke, E. K., Davies, T. J., Daru, B. H., Davis, C. C. 2018. Biological collections for understanding biodiversity in the Anthropocene. The Royal Society. Philosophical Transactions Royal Society B 374: 20170386.

Mona, M. H., El-Naggar, H. A., El-Gayar, E. E., Masood, M. F., Mohamed, E. S. N. 2019. Effect of human activities on biodiversity in Nabq Protected Area, South Sinai, Egypt. The Egyptian Journal of Aquatic Research 45, 33-43.

Munyai, T., Foord, S. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. Journal of Insect Conservation 16, 677-695.

Pavoine, S., Bonsall, M. B. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews 86, 792-812.

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M., Prentice, H. C. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. Journal of Ecology 101, 857-866.

Rovero, F., Marshall, A. R., Jones, T., Perkin, A. 2009. The primates of the Udzungwa Mountains: diversity, ecology and conservation. Journal of Anthropological Sciences 87, 93-126.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., Edwards, D. P. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31, 67-80.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33, 2-22.

Webb, C. O., Ackerly, D. D., McPeek, M. A., Donoghue, M. J. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33, 475-505.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30, 279-338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21, 213-251.

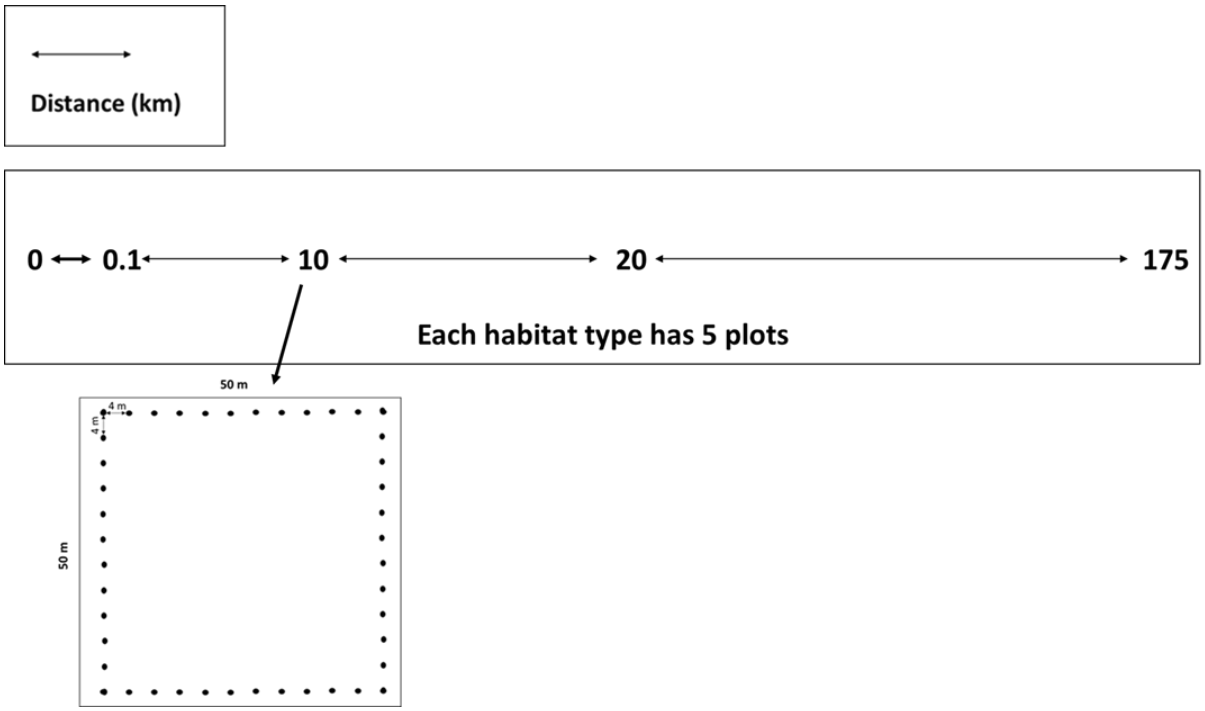
Whittaker, R. J., Willis, K. J., Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28, 453-470.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J. A., Harrison, S. P. 2010. Niche conservatism

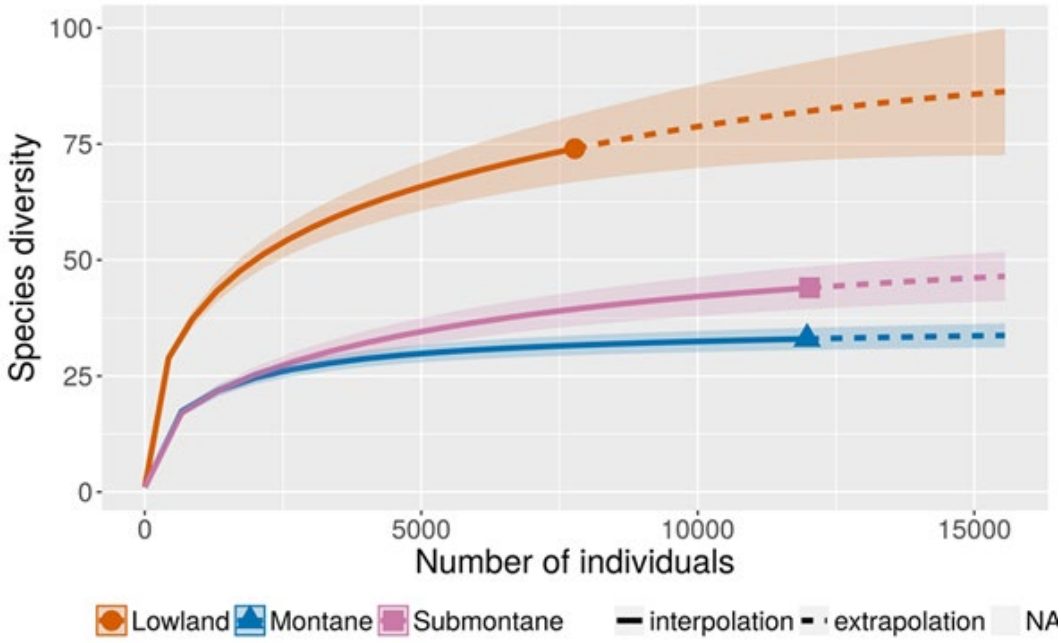
as an emerging principle in ecology and conservation biology. Ecology Letters 13, 1310-1324.

Wiens, J. J., Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36, 519-539.

APPENDIX A: The five (50m x 50m) plots consisting of 12 pitfall traps on each side of the plot 4 m apart at each elevation (lowland (300-800 m.a.s.l), sub-montane (800-1400 m.a.s.l), montane (1400-1500 m.a.s.l)).



APPENDIX B: Interpolation and extrapolation of species diversity at three forest types (lowland, sub-montane, montane) across the studied communities.



APPENDIX C: Checklist of subfamilies and ant species collected in three habitat types of the Udzungwa mountains ranges.

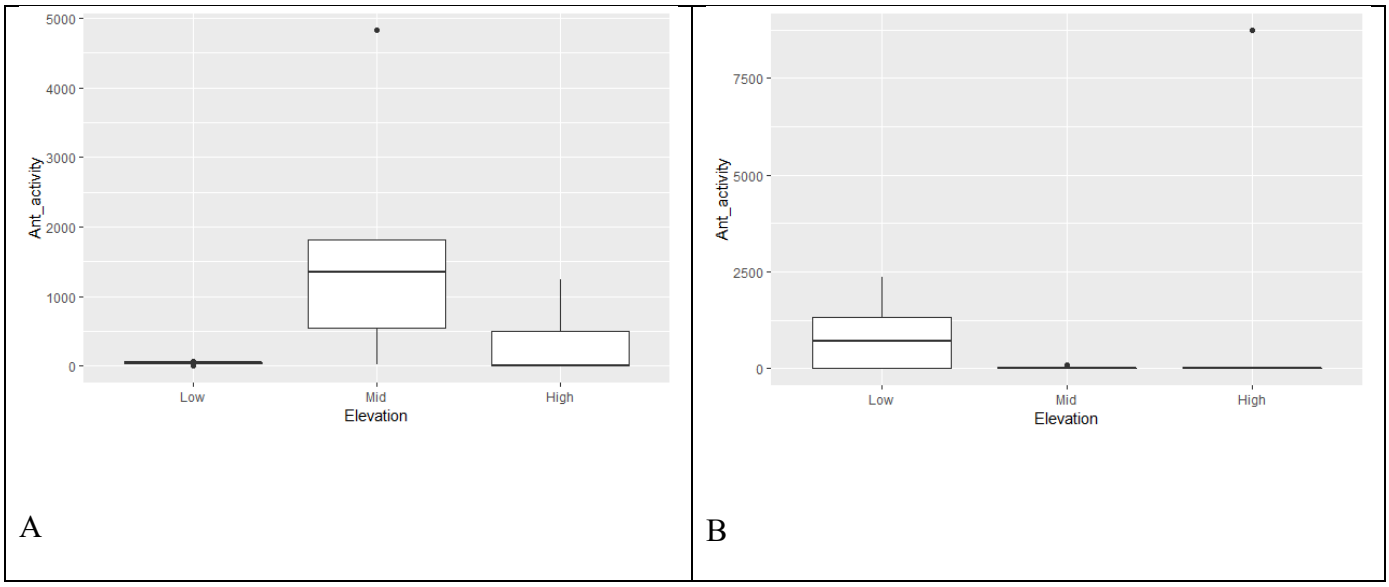
	Habitat type		
Subfamilies and species	Lowland	Sub-montane	Montane
Dolichodrinae			
Technomyrmex sp.01	2	0	0
Technomyrmex sp.02	1	0	0
Technomyrmex sp.03	0	1	0
Dorylinae			
Aenictus sp.01	0	2	0
Dorylus sp.01	4393	134	8733
Parasyscia sp.01	0	3	0
Parasyscia sp.02	0	1	0
Formicinae			
Camponotus sp.01 (*maculatus* gp.)	21	11	10
Camponotus sp.02 (*etiolipes* gp.)	16	1	0

Camponotus sp.03 (*cintellus* gp.)	1	0	0
Camponotus sp.04 (*maculatus* gp.)	5	0	0
Camponotus sp.05 (*niveosetosus* gp.)	1	2	0
Lepisiota cf. crinite	0	0	5
Lepisiota sp.01 (*capensis* gp.)	31	3	160
Lepisiota sp.02	3	0	0
Lepisiota sp.03	5	0	0
Lepisota sp.03	2	0	0
Nylanderia sp.01	137	18	0
Plagiolepis sp.01	5	0	0
Plagiolepis sp.02	2	0	0
Plagiolepis sp.03	0	0	1
Polyrhachis sp.01	8	6	0
Polyrhachis sp.02	1	0	0
Tapinolepsis sp.03	0	0	2
Tapinolepsis sp.01	1	0	0
Tapinolepsis sp.02	0	2	4
Myrmicinae			
Calyptomyrmex sp.01	0	1	0
Cardiocondyla sp.01	0	0	6
Carebara sp.01	11	9	0
Carebara sp.02	104	0	2
Catalaucus sp.01	0	1	0
Crematogaster sp.01	8	0	13
Crematogaster sp.02	5	0	0
Crematogaster sp.03	8	0	0
Crematogaster sp.04	4	6	5
Crematogaster sp.05	1	0	0
Melissotarsus emeryi	1	0	0
Meranoplus sp.01	7	0	0
Microdaceton sp.01	1	0	0
Monomorium sp.01	27	0	0
Myrmicaria sp.01	224	8539	1749

Pheidole sp.01 (*crassinoda* gp.)	181	895	641
Pheidole sp.02	351	548	11
Pheidole sp.03	348	6	0
Pheidole sp.04 (*megacephala* gp.)	699	401	193
Pheidole sp.05	85	0	0
Pheidole sp.06	8	115	18
Pheidole sp.07 (*liengmei* gp.)	225	0	0
Pheidole sp.08	15	3	0
Solenopsis sp.01	191	39	63
Solenopsis sp.02	9	3	0
Strumigenys sp.01	1	14	3
Strumigenys sp.02	4	6	0
Strumigenys sp.03	6	0	0
Strumigenys sp.04	0	21	21
Strumigenys sp.05	0	1	0
Strumigenys sp.06	0	0	6
Tetramorium cf. yarthiellum	104	0	0
Tetramorium sp.01 (*setigerum* gp.)	38	0	0
Tetramorium sp.02 (*setigerum* gp.)	1	0	0
Tetramorium sp.03 (*weitzeckeri* gp.)	125	738	95
Tetramorium sp.04 (*setigerum* gp.)	2	0	0
Tetramorium sp.05 (*gabonense* gp.)	16	0	0
Tetramorium sp.06	1	0	0
Tetramorium sp.07 (*notiale* gp.)	3	2	1
Tetramorium sp.08	1	0	0
Tetramorium sp.09	1	0	0
Tetramorium sp.10 (*sereceiventre* gp.)	1	0	0
Tetramorium sp.11 (*simillimum* gp.)	40	1	4
Tetramorium sp.12	1	0	0
Tetramorium sp.13	0	3	0
Tetramorium sp.14	0	0	40
Tetramorium sp.14 (*Rhpatomyrmex* gp.)	0	1	0
Tetramorium sp.15 (*notiale* gp.)	0	0	9

Tetramorium sp.16	0	0	6
Tetramorium sp.17 (*squaminode* gp.)	0	0	19
Monomorium sp.02	1	21	0
Ponerinae			
Anochectus sp.01	1	1	0
Anochectus sp.02	2	0	0
Anochectus sp.03	1	0	0
Asphinctopone Pilosa	2	0	0
Bothoponera sp.01	0	3	0
Bothroponera sp.01	10	60	0
Bothroponera sp.02	2	0	0
Bothroponera sp.03	3	1	0
Cryptopone sp.01	0	0	1
Hypoponera sp.01	1	0	0
Hypoponera sp.02	2	0	0
Hypoponera sp.03	0	0	6
Leptogenys sp.01	5	386	42
Leptogenys sp.02	0	2	0
Leptogenys sp.03	2	0	0
Leptogenys sp.04	0	0	12
Megaponera analis rapax	209	1	0
Mesoponera sp.01	3	0	0
Mesoponera sp.02	4	0	19
Mesoponera sp.03	4	5	0
*Odontomachu*s sp.01	8	0	0
Plectroctena sp.01	1	0	0
Plectroctena sp.02	0	4	0
Plectroctena sp.03	0	0	77

APPENDIX D: Ant activity of the two most influential species (A - *Myrmicaria rustica angustior,* B – *Dorylus helvolus*) across the elevational gradient – low (300-800 m), mid (800-1400 m), high (1400-1500 m).



APPENDIX E: Latitudinal and longitudinal coordinates for each plot.

Plot	Latitude	Longitude
1	- 7.41135	36.56286
2	-7.41149	36.56247
3	-7.41024	36.55493
4	-7.41052	36.55484
5	-7.40455	36.55069
6	-7.40421	36.55068
7	-7.41234	36.56007
8	-7.41129	36.55392
9	-7.41062	36.54524
13	-7.50296	36.52013
14	-7.50261	36.51330
15	-7.49398	36.50260
16	-8.30134	35.55089
17	-8.29581	35.54595
18	-8.29195	35.54273

APPENDIX F: A Venn diagram showing the number of species restricted and shared within the three forest types of the Udzungwa mountains.